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VERTEBRATE PALEONTOLOGY OF THE CLOVERLY FORMATION (LOWER CRETACEOUS), I: FAUNAL COMPOSITION, BIOGEOGRAPHIC RELATIONSHIPS, AND SAMPLING

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ABSTRACT—The vertebrate fauna of the Cloverly Formation has been studied for more than 75 years, but remains poorly sampled and incompletely understood. We undertook an extensive survey of the formation that resulted in the discovery of several new, highly productive vertebrate microfossil bonebeds (VMBs). Comprehensive sampling of these and other sites has nearly doubled the known vertebrate diversity of the Cloverly Formation. In addition to the comparatively well-known dinosaurs, this augmented faunal list includes hybodontoid sharks, numerous bony fishes, three lissamphibian lineages, lizards, multiple crocodylians, and several new mammal occurrences. The known Cloverly vertebrate fauna now more closely resembles those of other late Early Cretaceous formations in North America, indicating broad similarities across wide geographic areas at this time. In addition, this work underscores the important role VMBs can play in areas previously studied primarily through surface prospecting and quarrying, especially for assessing paleoecology and species diversity.

INTRODUCTION

Barnum Brown (Brown, 1933, 1935) and John Ostrom (Ostrom, 1970) prospected the Cloverly Formation of Wyoming and Montana over nearly four decades, seeking fossils that might bridge the Upper Jurassic and Upper Cretaceous terrestrial assemblages of North America. Their efforts yielded a unique, but low-diversity dinosaur fauna typified by the dromaeosaurid theropod *Deinonychus antirrhopus* and the basal euornithopod *Tenontosaurus tilletti* (Ostrom, 1969, 1970), but few non-dinosaurian vertebrates. The search for 'transitional' Early Cretaceous faunas later shifted to more productive formations, particularly the Cedar Mountain and Antlers (e.g., Winkler et al., 1990; Cifelli et al., 1997, 1999). These strata bracket the Cloverly geographically and record more upland (Cedar Mountain) to coastal (Antlers) paleoenvironments. Despite its historical significance, the Cloverly fauna remains poorly known, making it difficult to assess its full composition or biogeographic relationships.

Most known Cloverly species were discovered through traditional prospecting. Ostrom recovered several nearly complete dinosaur specimens but few other taxa—two lungfishes, an amioid, a crocodylian, and three to four turtles (Ostrom, 1970). Although he also attempted to recover mammals and other small vertebrates from his most productive quarries via screenwashing, this was relatively unsuccessful (Ostrom, 1970:1), and in fact the first known Cloverly mammal was found in concretions (Jenkins and Schaff, 1988). However, recently discovered microvertebrate-bearing deposits in Montana have yielded amphibians (Gardner, 1999), lepidosaurs (Nydam and Cifelli, 2002), juvenile dinosaurs (Maxwell and Horner, 1994), and additional mammals (Cifelli et al., 1998; Cifelli, 1999a), hinting that a comprehensive search for small vertebrates might result in higher recovered vertebrate diversity.

Beginning in 2003, one of us (M.T.C.) initiated a project to survey the Cloverly Formation for vertebrate microfossil bonebeds (VMBs; sensu Rogers and Brady, 2010). Such sites would significantly improve the uneven prior sampling of the Cloverly fauna by providing greater numbers of specimens representing a broader diversity of taxa. Furthermore, sufficiently large samples from isotaphonomic settings would permit exploration of species abundance, richness, and other ecological factors that are currently inaccessible for Cloverly vertebrates. Recovery of these data would, in turn, permit explicit comparisons with other Early Cretaceous faunas (e.g., Winkler et al., 1990; Cifelli et al., 1997, 1999).

In this paper (the first of two), we identify several taxa previously unknown from the Cloverly Formation and incorporate them into a revised faunal list. All sites are placed stratigraphically and associated with host lithologies, and the richest are analyzed individually using rarefaction (e.g., Tipper, 1979; Colwell and Coddington, 1994) to understand intraformational diversity variations. The result is a detailed, sample-rich assessment of the Cloverly fauna and its attributes. A more focused analysis of the Cloverly paleoecosystem, along with taphonomic assessments, will be presented in a forthcoming paper.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A.; **YPM**, Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

GEOLOGIC SETTING

Sedimentology and Paleoenvironment

Cloverly Formation outcrops occur from central Wyoming through central Montana, primarily in the Bighorn Basin (Fig. 1). Cloverly strata are typically 20–80 m thick and disconformably overlie the Upper Jurassic (to earliest Cretaceous?) Morrison

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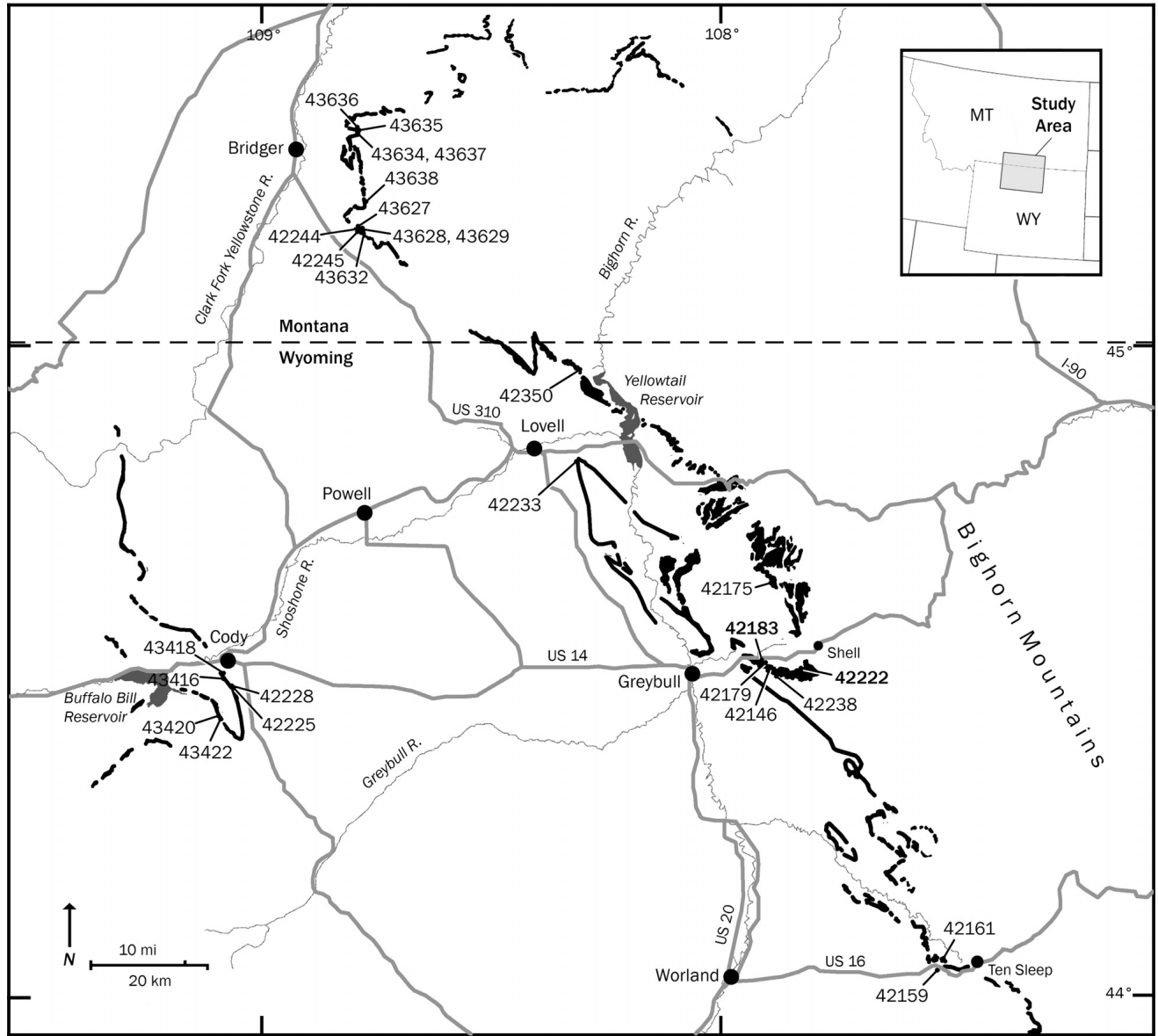
FIGURE 1. Map of the study area, Bighorn Basin. Cloverly Formation outcrops are shown in black. Locality numbers correspond with Table 1; VMBs are in bold. Inset: Study area location in Wyoming and Montana.

Formation (Zaleha, 2006). Conglomerates and sandstones typify the lower strata (May, 1993), whereas mudstones, diamictites, and wackes are more common up-sequence (Zaleha and Wiesemann, 2005). Clays, variably rich in illite, kaolinite, and smectite, give the upper half of the formation its characteristic variegated appearance (Zaleha, 2006). These upper levels also host polished extraformational clasts of chert, quartzite, and silicified limestone. Although these clasts have been likened to gastroliths, most are likely abiotic in origin (Zaleha and Wiesemann, 2005).

Zaleha and Wiesemann (2005) suggested that Cloverly sediments were deposited in lacustrine, fluvial, and playa settings. Moberly (1960) interpreted the lowest level as an erosional lag deposit, noting its underlying disconformity with the Morrison. Sedimentary structures in the lower conglomerates and sandstones suggest northeast-trending braided-channel deposits (May et al., 1995) representing streams of varying size and sinuosity (Meyers et al., 1992).

The higher levels of the Cloverly also include channel deposits, some of which were likely produced by hyperconcentrated and/or stratified river flows (Zaleha and Wiesemann, 2005). The latter often include pebble and cobble-sized 'gastroliths' suspended in fine-grained matrices. Although larger skeletal remains are occasionally associated with these mudflow deposits, small fossils at such sites are not concentrated but rather mixed among larger elements and can show preferred orientations.

In addition to these deposits, many outcrops of the middle and upper Cloverly are composed of fine-grained sediments that lack evidence of channel structure or significant flow. These are suggestive of lower-energy deposition, and were interpreted by Moberly (1960) as seasonal lake deposits that included weathering volcanic ash. Microvertebrate fossils, including tiny bone 'grains,' can occur as VMB concentrations within these clay- and mudstones. However, 'gastroliths' of any kind are uncommon, and the fossils typically lack a degree of polish or wear that would

indicate long-distance transport. We suggest that these VMBs accumulated as attritional deposits within quiet-water settings (Rogers and Brady, 2010).

Stratigraphic and Regional Structural Settings

Difficulties correlating disparate outcrops and identifying the Morrison–Cloverly contact have complicated efforts to divide the Cloverly Formation into formal stratigraphic units. Ostrom (1970) divided the region's Jurassic–Cretaceous sediments into eight units, assigning Units I–III to the Morrison, IV–VII to the Cloverly, and VIII to the overlying Sykes Mountain Formation. These correspond roughly with Moberly's (1960) subunits in the Bighorn Basin and with other Cloverly subdivisions in the Wind River Basin (e.g., Zaleha, 2006).

The lowermost Cloverly unit, composed of conglomerates and conglomeratic sandstones, has been referred to as the Pryor Conglomerate (Moberly, 1960), Unit IV (Ostrom, 1970), or Interval A (Zaleha, 2006). These basal conglomerates are commonly observed in the Wind River Basin (May et al., 1995) but are often absent in the Bighorn Basin (Moberly, 1960). The middle Cloverly unit is the Little Sheep Mudstone Member (Moberly, 1960) or Unit V (Ostrom, 1970), and consists of light-gray to red bentonitic mudstones. Vertebrate remains are more common in this unit (Moberly, 1960; Ostrom, 1970) along with chalcedony, quartz, and barite concretions (Ostrom, 1970). Moberly (1960) assigned upper Cloverly strata to the Himes Member, which Ostrom (1970) divided into coarse-grained sandstone channel deposits (Unit VI) and an extensive, brightly colored, cliff-forming claystone series (Unit VII). Zaleha (2006) assigned the Unit V sandstones and conglomerates to Interval B and the Unit V mudstones to Interval C. Thus, although it includes part of the Little Sheep Mudstone, Interval C corresponds primarily with the Himes Member.

Regionally, the Cloverly Formation was deposited in a narrow forebulge depozone formed during the Sevier Orogeny, east of a fold-and-thrust belt (Meyers et al., 1992; May, 1993; May et al., 1995; Zaleha and Wiesemann, 2005; Zaleha, 2006). The Sevier orogen has also been identified as the source for many Cloverly extraformational clasts, including the aforementioned 'gastroliths' (Zaleha and Wiesemann, 2005). As such, the formation may be laterally equivalent to the Garnett Group and Lakota Formation (Zaleha, 2006). The overlying Sykes Mountain Formation represents transgressive marine deposition, placing the Cloverly paleoenvironment near, although not directly at, a coastal margin (Moberly, 1960; Meyers et al., 1992).

Age of the Cloverly Formation

Constraining the age of the Cloverly Formation has also proven problematic. Ostrom (1970) assigned an Aptian–Albian age based on structural and vertebrate paleontological data. Fission-track dating of detrital zircons from Cloverly bentonites and tuffs has produced a wide range of ages. Uncorrected dates of 125–128 Ma were obtained for three sites in the Wind River Basin (May et al., 1995), although these may actually be from the Morrison Formation (M. D'Emic, pers. comm.). Samples from the northeastern Bighorn Basin have yielded dates with broad error ranges for the Little Sheep Mudstone (129 ± 16 Ma) and Himes Sandstone (119 ± 10 to 93 ± 8 Ma) (Chen and Lubin, 1997). Recent palynological and charophyte data support a Neocomian–Albian age (Zaleha, 2006), while magnetostratigraphy is consistent with a Neocomian–early Aptian age (May et al., 1995). Thus, there is general agreement that the uppermost Cloverly includes Aptian-age deposits. We are currently analyzing detrital zircon samples obtained from several of the sites documented here in an attempt to better define the age of the formation.

New Localities

New sites recorded here (Fig. 1) are placed within the prior stratigraphic framework (Ostrom, 1970) (Table 1). Most occur

TABLE 1.   New Cloverly Formation vertebrate localities.

USNM Loc.	7.5' Quad	Lithology	Unit	Collecting
42238	Manderson NE, WY	Gray claystone	Low V?	S
42244	Wade, MT	Dark gray claystone	Low V?	S
43627	Wade, MT	Dark gray mudstone	Low V?	S
43628	Wade, MT	Dark gray mudstone	Low V?	S
43629	Wade, MT	Dark gray mudstone	Low V?	S
43632	Wade, MT	Dark gray concretionary mudstone	Low V?	S
42146	Devils Kitchen, WY	5Y 7/1, blocky mudstone	Low V	S, B
42179	Devils Kitchen, WY	White-gray claystone	V	S
42183	Devils Kitchen, WY	N5, intraclastic, blocky claystone	V	S, B
42222	Manderson NE, WY	5Y 7/1, laminated claystone with N8 mottling	V	S, B
43416	Indian Pass, WY	Red claystone	V	S, T
43418	Indian Pass, WY	Green-gray sandy claystone with some lamination	V	S, B
43420	Indian Pass, WY	Green-gray flaggy claystone	V	S, B
42225	Indian Pass, WY	Green-gray and blue-gray flaggy claystones	V	S, T
42228	Indian Pass, WY	Gray claystone	V	S
42233	Lovell Lakes, WY	Green-gray bentonitic, intraclastic claystone	V	S, B, J
43634	Bluewater, MT	Medium gray claystone	V	S
43635	Bluewater, MT	Dark gray mudstone	V	S
43636	Bluewater, MT	Dark gray claystone	V	S
43637	Bluewater, MT	Dark gray mudstone	V	S
43638	Wade, MT	Red and gray mudstone	V	S
42350	Sykes Spring, WY	5Y 6/4, silty claystone with plant hash	High V	S
42245	Wade, MT	Red claystone	High V	S
42161	Wild Horse Hill, WY	Gray mudstone	Low VI	S
42159	Wild Horse Hill, WY	Green-gray claystone	VI	S, B
42175	Bear Creek Ranch, WY	Tan sandy mudstone above white claystone	VI	S, B
43422	Indian Pass, WY	Blue-gray blocky claystone	VII?	S, B

Locations are shown on Figure 1 and listed here with reference to the relevant USGS 7.5' quadrangle; exact geographic coordinates are kept on file in the Department of Paleobiology, National Museum of Natural History, and are available to qualified researchers. These are listed according to stratigraphic unit, from lowest to highest (Ostrom, 1970). **Abbreviations**: **B**, bulk; **J**, jacket; **Loc.**, locality; **S**, surface; **T**, test.

in the middle and upper levels of Unit V, including the VMBs. Exceptions include USNM Localities (Locs.) 42159, 42161, and 42175, which are in Unit VI, and USNM Loc. 43422, which we place in Unit VII. Within Unit V, USNM Loc. 42146 and many Montana sites are low in section whereas USNM Locs. 42245 and 42350 occur near the top.

The localities around Shell occur in the white claystones of Unit V and are close to Ostrom's ledge-forming 'tuff' (Ostrom, 1970). Other site lithologies tend toward darker-colored claystones and mudstone (Table 1). USNM Locs. 42183 and 42222 are discrete, fossil-bearing lenses near the surface of small hillocks. Fossiliferous horizons are also exposed at USNM Locs. 42179, 42244, and 43632, but we were not able to identify a host stratum at all sites. Fossils at USNM Locs. 42175 and 43422 were resting on nearly barren strata; we inferred that they represented present-day deflation-lag accumulations derived from now-eroded host strata. The presence of a dark hematitic crust on most fossils from these sites suggests that they accumulated on a floodplain and were subjected to pedogenic processes prior to burial (Bown and Kraus, 1981a, 1981b).

Abundant invertebrate fossils were found but are not discussed in detail here. Bivalves are abundant in lower Cloverly strata but uncommon in the upper levels. At least three distinct taxa are present, presumably representing freshwater or possibly estuarine animals. Gastropod fossils typically co-occur with abundant bivalves and are also rare in the upper levels of the formation. Crayfish gastroliths are common in several sites (Huxley, 1880b; D. Brinkman, pers. comm.).

METHODS

The specimens reported here were obtained through fieldwork conducted from 2003 to 2010, during which we discovered more than 40 new sites yielding identifiable vertebrate fossils and visited a number of previous quarries (Ostrom, 1970). Sites with abundant small bones on the surface were tested by screen-washing and sorting a small bulk sample, typically ca. 5 kg (Table 1). Nine sites (USNM Locs. 42146, 42159, 42175, 42233, 43418, 43420, 43422, 42183, and 42222) proved sufficiently productive to warrant more extensive sampling. The latter two were especially rich and can be considered VMBs (sensu Rogers and Brady, 2010). Both continue to produce fossils.

We collected large bulk samples (100–1500 kg) from these nine sites and screenwashed them once in the field to concentrate the samples. The residues were shipped to the Department of Paleobiology's Vertebrate Preparation Laboratory in the Smithsonian's National Museum of Natural History, where the fossils were removed manually. Each specimen was identified anatomically and categorized at the lowest possible taxonomic level, often with the aid of a binocular microscope (Zeiss Stemi SV 6) or scanning electron microscope (Philips XL-30 environmental scanning electron microscope [ESEM]; Hitachi TM3000). We aggregated specimen counts by taxon, sorted them into taxonomically nested sets (e.g., counts of *Deinonychus* figured into the count for Theropoda, but not vice versa), and tallied specimen and taxon counts per site. The resulting faunal list (Table 2) reflects contributions from all known Cloverly sites, including a small, unreported collection of screenwashed fossils from Ostrom's (1970) locality 63-19 ('site 118') in the YPM collections.

We analyzed assemblage (locality-level) and faunal (formation-level) samples using rarefaction (sensu Jamniczky et al., 2003, and references therein) using Analytic Rarefaction 2.0 (Holland, 2010) at 10-specimen increments for three different sampling regimes: (1) sampling across all sites (= formation aggregate), using the total faunal list and specimen counts; (2) three independent sample-rich sites (bulk-sampled counts only)—USNM Locs. 42183, 42222, and 42175; and (3) the complete published Cloverly macrofossil sample (compiled

TABLE 2. Complete faunal list for the Cloverly Formation, with diversities of major taxonomic groups.

Taxon	Total	VMB
CHONDRICHTHYES	5	4
Elasmobranchii		
Hybodontidae		
Egertonodus sp.*		
*Hybodus parvidens**		
Lonchidiidae*		
Parvodus sp.*		
Lonchidion sp.*		
Myliobatiformes		
Myliobatidae		
Pseudohypolophus sp.		
OSTEICHTHYES	6	6
Actinopterygii	4	4
aff. Pycnodontidae*		
Holostei		
Semionotidae*		
aff. *Lepidotes* sp.*		
Amiiformes indet.*		
Vidalamiinae indet.*		
Sarcopterygii	2	2
Ceratodontidae		
Ceratodus frazieri		
Ceratodus cf. *C. guentheri**		
LISSAMPHIBIA	5	5
Albanerpetontidae	1	1
Albanerpeton, n. sp.*		
Caudata*	2	2
cf. Scapherpetontidae*		
Batrachosauroididae*		
Anura*	2	2
cf. *Scotiophryne* sp.*		
Anura indet., species A*		
REPTILIA	26	20
Testudinata	4	3
Solemydidae		
Naomichelys speciosa		
?Glyptopsinae		
"*Glyptops*" *pervicax*		
Testudinata indet., species A*		
Cryptodira indet.		
Squamata	4	4
Paramacellodidae		
Paramacellodus keebleri		
Paramacellodidae? indet., species A*		
Teiidae*		
*Ptilotodon wilsoni**		
Teiidae indet., species A*		
Crocodyliformes	4	4
cf. Bernissartidae*		
cf. Atoposauridae*		
cf. Goniopholididae		
cf. Pholidosauridae*		
Dinosauria	14	9
Theropoda	7	5
Tetanurae		
Acrocanthosaurus atokensis		
Dromaeosauridae		
Deinonychus antirrhopus		
?Ornithomimidae indet.		
Oviraptorosauria		
Microvenator celer		
Theropoda indet., species A*		
Theropoda indet., species B*		
?Aves*		
Sauropoda	2	1
Titanosauriformes indet.		
Rugocaudia cooneyi		
Sauroposeidon proteles		
Ornithopoda	2	2
cf. *Zephyrosaurus* sp.		
Iguanodontia		
Tenontosaurus tilletti		

TABLE 2. Complete faunal list for the Cloverly Formation, with diversities of major taxonomic groups. (*Continued*).

Taxon	Total	VMB
Ankylosauria	2	1
Nodosauridae		
Sauropelta edwardsi		
Ankylosauridae		
Tatankacephalus cooneyorum		
Ceratopsia indet.	1	0
MAMMALIA	9	8
Eutriconodonta	2	2
Alticonodontinae		
Corviconodon montanensis		
Gobiconodontidae		
Gobiconodon ostromi		
Multituberculata*	3	3
Cimolodonta*		
?*Paracimexomys* sp.*		
Bryceomys sp.*		
Plagiaulacida*		
Janumys sp.*		
Symmetrodonta*	1	1
Spalacotheriidae*		
Trechnotheria	3	2
Montanalestes keeblerorum		
Metatheria indet.*		
cf. *Atokatheridium* sp.*		
cf. *Oklatheridium* sp.*		
Totals	51	43

Asterisks indicate newly added taxa; underlined taxa were previously known but not recovered in the present study. **Abbreviation**: **VMB**, subset of diversity recovered from vertebrate microfossil bonebeds in the present study.

from the literature and entered into the Paleobiology Database; www.paleodb.org). This last represents a point of comparison between the results of traditional sampling (prospecting and quarrying) and VMB collection (screenwashing and associated techniques).

Taxonomic abundances are difficult to determine from VMB samples due to the manner in which these sites likely accumulated (cf. Rogers and Brady, 2010). Using minimum numbers of individuals (MNIs) underestimates the original number of organisms, because few VMB specimens are likely to derive from the same individual (Carrano and Velez-Juarbe, 2006). Conversely, raw specimen counts can introduce biases due to taxonomically driven differences in skeletal element counts, and therefore potential contributions to the sample. We used raw specimen counts as a baseline for abundance comparisons, but made allowances for element count differences (which we assessed using extant representatives of major groups).

We assessed biogeographic relationships by calculating Sørensen Index values (sensu Wolda, 1981) between several Lower Cretaceous units: the Cloverly, Antlers, Patuxent (Arundel Clay facies), and Cedar Mountain (Mussentuchit Member) formations. The Sørensen formula generated index values between 0 (indicating complete faunal dissimilarity) and 1 (indicating complete similarity) for each pair of strata. Taxonomic diversities for non-Cloverly strata were obtained from the published literature via the Paleobiology Database. We conducted interformational comparisons at two levels of specificity. First, we counted taxa as similar if they matched at any level of taxonomic identification (e.g., Atoposauridae indet. in multiple formations). Second, we only counted taxa as similar if they belonged to the same genus.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880a
ELASMOBRANCHII Bonaparte, 1838

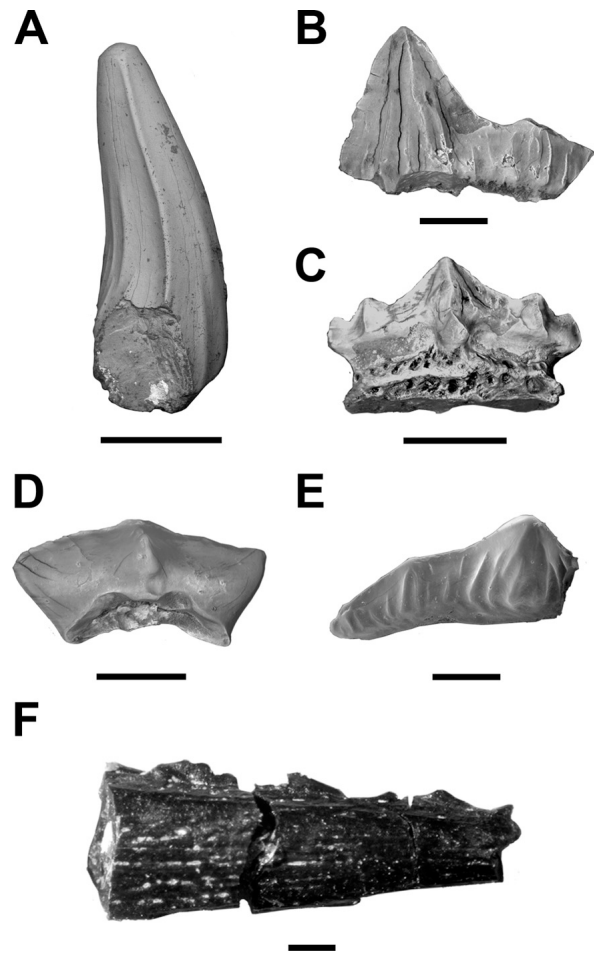
FIGURE 2. Chondrichthyans from the Cloverly Formation. **A**, USNM 546504, *Egertonodus* sp., central cusp, lingual view; **B**, USNM 546506, *Hybodus parvidens*, partial tooth, labial view; **C**, USNM 546507, *Parvodus* sp., tooth, labial view; **D**, USNM 546505, *Lonchidion* sp., tooth, labial view; **E**, USNM 546503, Hybodontoidea indet., partial tooth, lingual view; **F**, USNM 546673, Hybodontoidea indet., dorsal spine, lateral view. Scale bars equal 0.5 mm.

HYBODONTOIDEA (Agassiz, 1843)
HYBODONTIDAE Agassiz, 1843
EGERTONODUS Maisey, 1987
EGERTONODUS sp.
(Fig. 2A)

Localities—USNM Locs. 42175, 42183.
Material—32 partial teeth.
Description—The robust central cusps of these teeth are 1–4 mm in height and sigmoidally curved in lateral view, an apomorphy of *Egertonodus* (Rees, 2002). Sharp carinae separate the broad, only slightly convex labial face from the more convex lingual face, as in *E. basanus* (Rees, 2002). Robust, widely spaced vertical folds extend from near the crown base roughly halfway to the apex on both labial and lingual sides of smaller specimens, but the labial face is nearly smooth in the largest specimens (Fig. 2A). Many of the folds trend toward one another apically and/or bifurcate basally. The labial folds are more pronounced and frequently terminate in knob-like projections at the crown base.

HYBODUS Agassiz, 1837
HYBODUS PARVIDENS Woodward, 1916
(Fig. 2B)

Localities—USNM Locs. 42175, 42183.

Material—17 partial teeth.

Description—These specimens are distinguished by a relatively short central cusp (1–2 mm tall) with two lateral cusplets and coarse folds that extend nearly to the subrounded apex (Fig. 2B). The cusps are not labiolingually compressed and typically bear four inconsistently arranged labial folds, some of which converge toward a central, vertically oriented keel. These teeth resemble *H. parvidens* in their cusp proportions and the lack of strong mediolateral compression (Estes and Sanchíz, 1982). Cloverly specimens show some gradation from higher to lower central cusps, consistent with the monognathic heterodonty of this species (Rees, 2002).

LONCHIDIIDAE Herman, 1977
PARVODUS Rees and Underwood, 2002
PARVODUS sp.
(Fig. 2C)

Locality—USNM Loc. 42183.

Material—One tooth.

Description—The single specimen (USNM 546507) has a bulbous labial process and two pairs of closely spaced lateral cusplets placed far from the triangular central cusp (Fig. 2C). All five cusps are angular, with coarse vertical grooves between them on the labial and lingual surfaces. A porous root structure with visible foramina is separated from the crown by a pronounced constriction. The mesiodistal width (1.3 mm) is greater than the combined height of crown plus root.

LONCHIDION Estes, 1964
LONCHIDION sp.
(Fig. 2D)

Localities—USNM Locs. 42183, 42222.

Material—31 teeth.

Description—These teeth have a low, rounded principal cusp that is labiolingually compressed and curved slightly lingually. Peg-like labial processes are present. The occlusal crest has upturned ends and a weakly sinusoidal outline in lateral view. Most examples lack vertical folds and lateral cusplets (Heckert, 2004), although the latter do appear on specimens where the occlusal crest curves upward abruptly, providing evidence of heterodonty. Crown width ranges from 1 to 1.5 mm. Features consistent with the genus *Lonchidion* include crown constriction near the root (Sánchiz-Hernández et al., 2007) and a tricuspid shape (Estes et al., 1969) (Fig. 2D). The tiny size of these specimens is similar to *L. anitae* (Thurmond, 1971) and *L. microselachos* (Estes and Sanchíz, 1982:fig. 2).

HYBODONTOIDEA indet.
(Fig. 2E, F)

Localities—USNM Locs. 42175, 42183, 42222.

Material—213 partial teeth, four partial dorsal fin spines, one cephalic spine.

Description—Hybodontoid tooth fragments include isolated central cusps and lateral cusplets bearing vertical folds or striations (Fig. 2E). The dorsal spine fragments have vertical striae and a single row of posterior denticles (Fig. 2F). Although many *Hybodus* spines bear a double row of denticles (e.g., Thurmond, 1971; Bonde, 2004), this is more evident toward the spine base, and the present specimens may simply lack the relevant portions. Alternatively, these specimens may represent *Lissodus* and/or *Lonchidion*, which have dorsal spines bearing a single row of denticles for at least part of their length (Rees and Underwood, 2002). Each denticle is ~1 mm long, with a 3:1 length:width ratio, and either overlaps the next or abuts it, unlike the small, widely spaced denticles of *Hybodus* sp. (Agirrezabala et al., 1985:fig. 4). The cephalic spine (USNM 546466) has a long, posteriorly curved
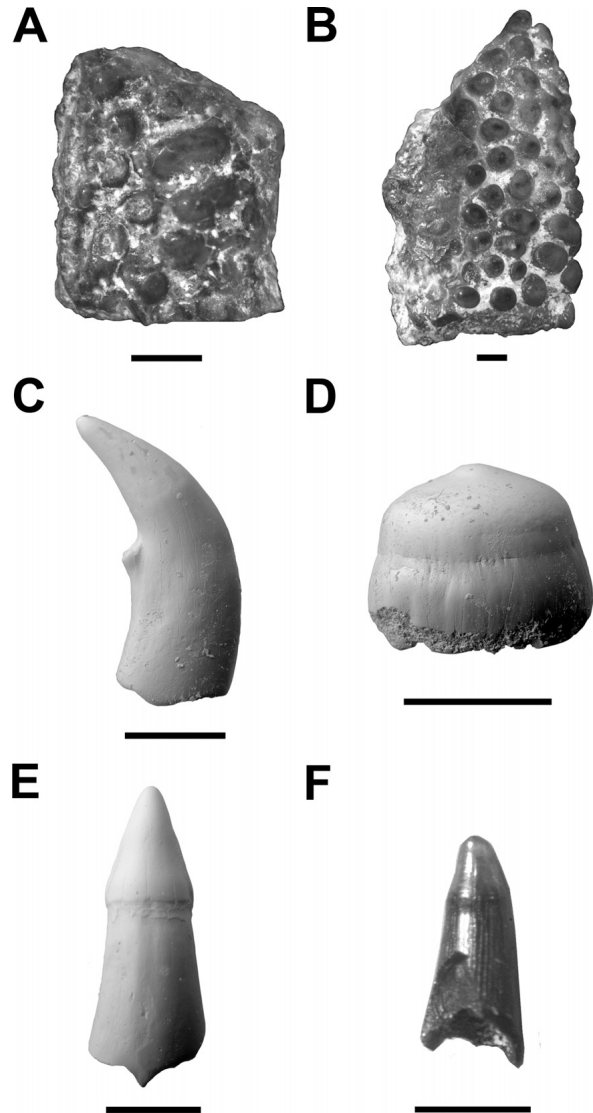

FIGURE 3. Actinopterygians from the Cloverly Formation. **A**, USNM 546510, aff. Pycnodontiformes indet., vomer fragment, occlusal view; **B**, USNM 546677, aff. Pycnodontiformes indet., vomer, lateral view; **C**, USNM 546511, *Lepidotes* sp., branchial tooth, lateral view; **D**, USNM 546512, *Lepidotes* sp., crushing tooth, lateral view; **E**, USNM 546513, Vidalamiinae indet., tooth, labial/buccal view; **F**, USNM 546514, Amiiformes indet., tooth, lingual/buccal view. Scale bars equal 1 mm (**A–B**, **D–F**) and 0.5 mm (**C**).

projection and an enlarged base with weak dorsal rugae but no flanges. A central foramen bisects the ventral surface.

OSTEICHTHYES Huxley, 1880a
ACTINOPTERYGII Cope, 1887
PYCNODONTIFORMES Berg, 1937
aff. PYCNODONTIDAE Agassiz, 1833
Gen. et sp. indet.
(Fig. 3A, B)

Localities—USNM Locs. 42183, 42222.

Material—Five partial vomers.

Description—These elements bear multiple, rounded teeth but differ in the size, arrangement, and number of teeth preserved. One specimen (USNM 546510) has elongate crowns surrounded

by smaller, circular teeth (Fig. 3A), whereas others show a more uniform tooth-size distribution (Fig. 3B). Some teeth resemble those of *Proscinetes* (Thies and Mudroch, 1996:pl. 1, fig. 8) and *Macromesodon* (Barck, 1992:fig. 6A; Thies and Mudroch, 1996:pl. 2, figs. 1, 2) but differ slightly from these taxa. Only vomer fragments are described here, but some tooth plates assigned to Actinopterygii (see below) may also derive from pycnodonts.

HOLOSTEI Müller, 1846 (sensu Grande, 2010)
SEMIONOTIFORMES Arambourg and Bertin, 1958
SEMIONOTIDAE Woodward, 1890
LEPIDOTES Agassiz, 1833
aff. *LEPIDOTES* sp.
(Fig. 3C, D)

Localities—USNM Locs. 42183, 42222.
Material—One branchial tooth, seven crushing teeth.
Description—Two types of semionotid teeth are present. The branchial tooth (USNM 546511) has a circular base, lacks ornamentation, and has a curved, asymmetrically placed primary cusp (Fig. 3C). Crushing tooth crowns are dorsoventrally flattened with wide occlusal surfaces (Fig. 3D). Unlike superficially similar actinopterygian teeth (see above), unworn *Lepidotes* crushing teeth have a small projection at the center of the occlusal surface, resembling an undeveloped central cusp. *Lepidotes* is a widespread taxon with a convoluted species-level taxonomy that we do not attempt to navigate here, but Cloverly specimens are similar to those reported elsewhere (e.g., Barck, 1992; Kriwet et al., 1997; Rees, 2002).

AMIIFORMES Hay, 1929
AMIIDAE Bonaparte, 1841
VIDALAMIINAE Grande and Bemis, 1998
Gen. et. sp. indet.
(Fig. 3E)

Localities—USNM Locs. 42183, 42222.
Material—17 teeth.
Description—These teeth possess labial and lingual carinae that expand downward from the apex (Fig. 3E), have transparent tips, and could derive from the dentary, premaxilla, maxilla, vomer, or dermopalatine. They are referred to Vidalamiinae based on the combined presence of an arrowhead-shaped tip and well-developed carinae (Grande and Bemis, 1998).

AMIIFORMES indet.
(Fig. 3F)

Localities—USNM Locs. 42175, 42183, 42146, 42222.

Material—94 teeth, eight partial maxillae/vomers, five partial ?ectopterygoids, one partial ?dermopalatine, one vertebra.
Description—Although difficult to identify, fragments with small conical teeth might represent ectopterygoids, endopterygoids, or metapterygoids, whereas others with a more chaotic small-tooth arrangement may be parasphenoids (Grande and Bemis, 1998). Numerous isolated teeth have tapered crowns, a horizontal basal cingulum, and transparent tips, and lack carinae as well as the basal striae that might indicate lepisosteiform affinities (Fig. 3F). They are similar to premaxillary teeth of *Amia calva* and *Ionoscopus* (Thies and Mudroch, 1996:pl. 2, fig. 5) and are smaller and more robust than those referred to Vidalamiinae, and therefore probably represent at least one additional amiiform taxon.

HOLOSTEI indet.
(Fig. 4A–C)

Localities—USNM Locs. 42175, 42183, 42222, 43420, 43422.
Material—731 'morphotype A' scales, 160 'morphotype B' scales, 66 'morphotype C' scales, 13 'morphotype D' scales.
Description—Four distinct ganoid scale morphotypes are present, which may derive from different portions of a single taxon or from different taxa represented here by other elements. 'Morphotype A' is thin (usually ≤1 mm) and diamond-shaped with concentric ornamentation (Fig. 4A). 'Morphotype B' has an interlocking joint and often features an internal surface ridge (cf. Brinkman, 2002) (Fig. 4B). Most specimens are rhombohedral and longer than wide, although there is some variation in shape. The largest scales are nearly 5 mm long. 'Morphotype C' are thick, elongate rhomboids with a scalloped posterior margin and a dark enameled surface (cf. Schultze, 1996; Brinkman, 2002) (Fig. 4C). 'Morphotype D' has concentric external surface rings and a rounded posterior projection overlain by two curved, lateral projections. It resembles some palaeoniscoid scales (Heckert, 2004:fig. 15E) as well as the mid-abdominal scales of *Lepisosteus osseus* (Grande, 2010).

ACTINOPTERYGII indet.

Localities—USNM Locs. 42175, 42183, 42222, 43420.
Material—125 teeth, 55 fin-ray segments.
Description—Most of these teeth have rounded occlusal surfaces that range from hemispheric with thick enamel and constricted bases to subrounded and cylindrical. The apices of the latter specimens are flattened, similar to the crushing teeth of *Lepidotes* (Barck, 1992:fig. 6F) but lacking an occlusal projection. Specimens with a basal crown constriction and circular profile are
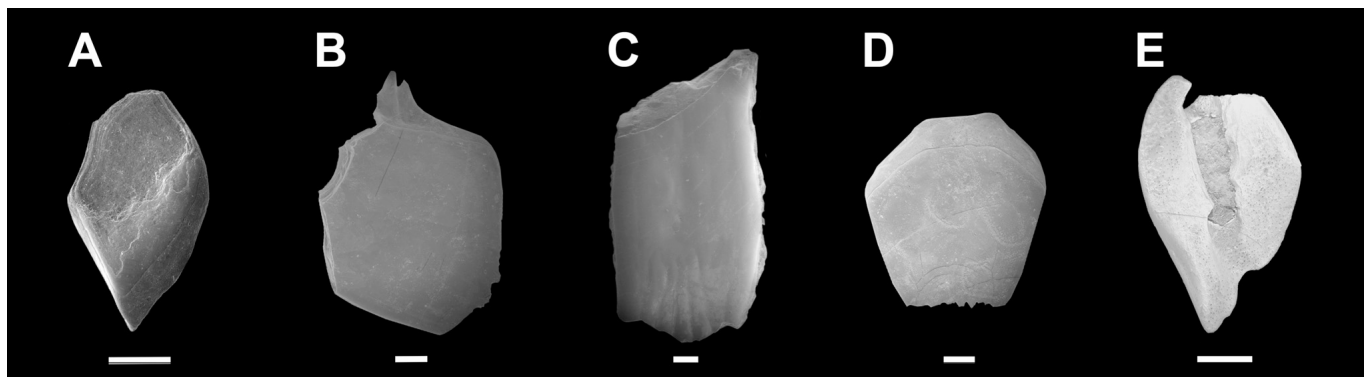

FIGURE 4. Osteichthyan scales from the Cloverly Formation. **A**, USNM 546675, Holostei indet. 'morphotype A,' internal? view; **B**, USNM 546676, Holostei indet. 'morphotype B,' external view; **C**, USNM 546509, Holostei indet. 'morphotype C,' external view; **D**, USNM 546674, Osteichthyes indet. 'morphotype A,' external view; **E**, USNM 546508, Osteichthyes indet. 'morphotype B,' internal view. Scale bars equal 0.5 mm.

similar to certain neopterygian teeth (e.g., "tooth morphotype 2" of Buscalioni et al., 2008:fig. 5). Thirteen teeth from USNM Loc. 42183 and 13 from USNM Loc. 42222 resemble amiid teeth in having clear, subpointed apices, but a slight constriction separates the crown from the base. Other teeth are similar to those of Gyrodontidae (Thies and Mudroch, 1996:pl. 1, figs. 1–3) and show variation suggestive of multiple taxa.

SARCOPTERYGII Romer, 1955
DIPNOI Müller, 1846
CERATODONTIDAE Gill, 1872
CERATODUS Agassiz, 1838
CERATODUS FRAZIERI Ostrom, 1970
(Fig. 5A)

Localities—USNM Locs. 42183, 42222, 43628.
Material—Four partial tooth plates.
Description—In *C. frazieri* tooth plates, the radial ridges extend onto four robust, non-tuberculate projections that diverge laterally, but disappear well before reaching the medial margin (Fig. 5A). The plates tend to be large, with proportionally short radial ridges. The most complete specimen (USNM 546680) is 26+ mm long, 16 mm wide, and ca. 4 mm thick. Ostrom (1970) noted that the anterior-most dental plate ridge terminates on the longest lateral projection in *C. frazieri*. This can be inferred for the most complete specimen, which preserves the two posterior projections and part of the two anterior projections.

CERATODUS cf. *C. GUENTHERI* Marsh, 1878a
(Fig. 5B)

Localities—USNM Locs. 42183, 42222, 43632.
Material—Eight partial tooth plates.
Description—These fragments compare favorably with the Late Jurassic *C. guentheri* based on their gracile projections and prominent medial ridges (Fig. 5B). As in *C. guentheri*, the external projections are sharply crested and taper distally, exhibiting a high length:width ratio (ca. 5:2 on a fairly complete specimen, USNM 546679). These projections account for roughly half of the plate length, and medially, the ridge crests extend almost to the internal margin. They differ from typical examples of *C. frazieri* and are best compared with *C. guentheri*; however, lacking a complete tooth plate, we are reluctant to refer these specimens to a Jurassic taxon

CERATODUS sp.

Localities—USNM Locs. 42183, 42222.
Material—12 tooth plate fragments.
Description—Several lungfish tooth plates are too incomplete to assign to a particular species, but they show *Ceratodus* synapo-

morphies such as a pitted occlusal surface texture, medial ridges, and/or evidence of a single prearticular sulcus (Soto and Perea, 2010).

OSTEICHTHYES indet.
(Fig. 4D, E)

Localities—USNM Locs. 42175, 42183, 42146, 42222, 43416, 43420, 43422, 42225; YPM Loc. 63–19.
Material—2111 indeterminate scales, six 'morphotype A' scales, 10 'morphotype B' scales, 34 teeth, four partial maxillae/dentaries, two partial vomers, 13 ?skull elements, three spines, 71 vertebral centra.
Description—Osteichthyan specimens are quite common but are difficult to assign to particular groups. Two distinct scale morphotypes are present: 'morphotype A' is thin and hexagonal with a slightly scalloped posterior margin (Fig. 4D); 'morphotype B' is proportionally thicker, more irregularly polygonal, and bears a deep groove on the internal surface (Fig. 4E). These scales may actually represent a fifth holostean scale morphotype. Osteichthyan teeth, spines, and enamel-covered skull elements are also present, but vertebral centra are rare and usually too poorly preserved to determine facet size or orientation. These amphicoelous centra are referred to Osteichthyes based on their circular articular surfaces and large height-to-anteroposterior width ratio. One maxilla fragment and several of the centra might pertain to Teleostei, but further study is required.

LISSAMPHIBIA Haeckel, 1866
ALLOCAUDATA Fox and Naylor, 1982
ALBANERPETONTIDAE Fox and Naylor, 1982
ALBANERPETON Estes and Hoffstetter, 1976
ALBANERPETON, n. sp.
(Fig. 6)

Localities—USNM Locs. 42175, 42183, 42222.
Material—18 partial premaxillae, 93 partial dentaries, 14 partial maxillae, 10 partial maxillae/dentaries, one pair of fused frontals, 14 axes, 23 partial humeri.
Description—The present materials appear to derive from a single species that is close to, but not identical with, *Albanerpeton arthridion* (Gardner, 1999). The unfused premaxillae are similar to those of *A. arthridion* (Gardner, 1999), and one specimen (USNM 546682) preserves a divided suprapalatal pit on the medial pars dorsalis (Fig. 6A). The dentary is broadly curved mediolaterally and exhibits a marked symphyseal eminence; the subdental shelf deepens posteriorly at a rate intermediate between *A. arthridion* and the Wessex Formation taxon (Fig. 6B; Gardner, 1999; Sweetman and Evans, 2011). The fused frontals (USNM 546683) resemble those of other species of *Albanerpeton* and the Wessex taxon (Sweetman and Evans, 2011) in their broadly triangular shape, but are closer to the former in having a wider internasal process and more prominent anterolateral processes (Fig. 6C, D). The postcranial elements are more difficult to identify to genus level and are tentatively assigned. The humeri are slender-shafted with a wide distal end that bears a large, hemispherical radial condyle, a marked ectepicondyle, and a small ulnar condyle (Fig. 6E). Some fragmentary amphibian specimens might derive from this taxon, including the hourglass-shaped dorsal vertebrae, which are too poorly preserved to allow recognition of the weakly developed anterior basapophyses characteristic of *Albanerpeton* (Estes and Sanchíz, 1982). No quadrates, parietals, or atlantal centra with albanerpetontid characters (Estes and Sanchíz, 1982; Gardner, 1999, 2000:fig. 2) have been identified.

URODELA Duméril, 1806
cf. SCAPHERPETONTIDAE Auffenberg and Goin, 1959
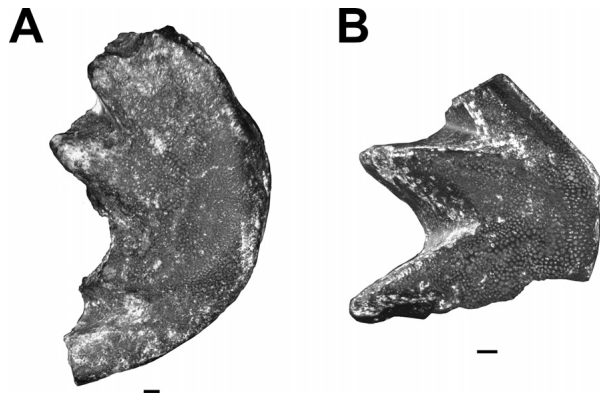Gen. et sp. indet.
(Fig. 7A, B)

FIGURE 5. Dipnoans from the Cloverly Formation. **A**, USNM 546680, *Ceratodus frazieri*, dental plate, occlusal view; **B**, USNM 546679, *Ceratodus* cf. *C. guentheri*, dental plate, occlusal view. Scale bars equal 1 mm.
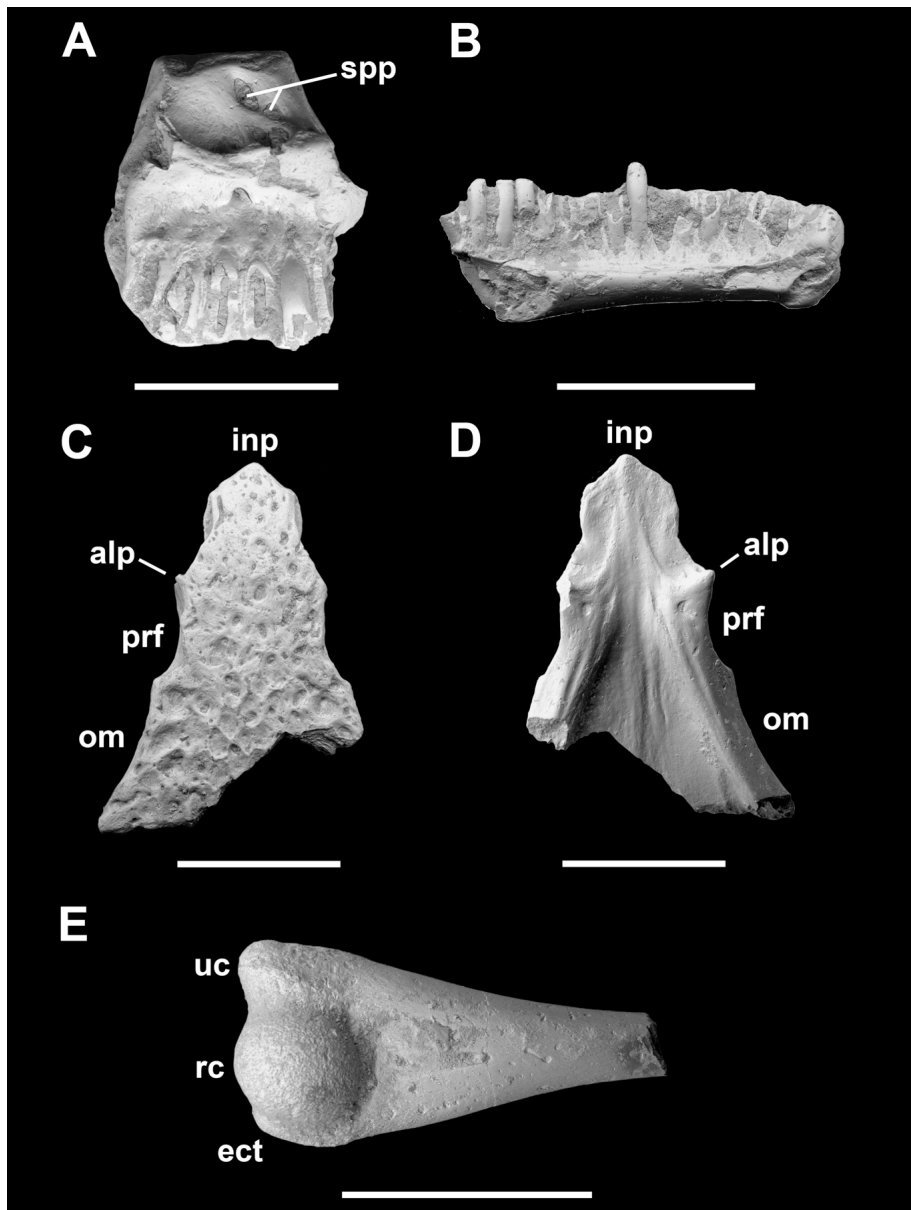
FIGURE 6. *Albanerpeton* sp. from the Cloverly Formation. **A**, USNM 546682, right premaxilla, medial view; **B**, USNM 546691, anterior left dentary, medial view; **C**, USNM 546683, frontals, dorsal view; **D**, USNM 546683, frontals, ventral view; **E**, USNM 546684, distal left humerus, posterior view. **Abbreviations**: **alp**, anterolateral process; **ect**, ectepicondyle; **inp**, internasal process; **om**, orbital margin; **prf**, prefrontal contact; **rc**, radial condyle; **uc**, ulnar condyle; **spp**, suprapalatal pit. Scale bars equal 1 mm.

Localities—USNM Locs. 42183, 42222.

Material—Two partial dentaries, four partial jaw elements, nine atlantes.

Description—None of the jaw fragments preserve teeth; they are compared with this family based on their size and robustness. The tooth sockets approach 0.25 mm in width on the largest specimen, roughly 3 times that seen in *Albanerpeton*. The dentary has a smooth lateral surface and a pronounced Meckelian groove that narrows anteriorly (Fig. 7A). Atlantal centra have a rounded odontoid process in dorsal view (Fig. 7B). The articular cotyles are circular in anterior view; in dorsal view their surfaces decline posteriorly ca. 45° to the anteroposterior axis of the bone (cf. Gardner, 2005:fig. 10.1). The centrum bears distinct ventral pits (cf. Brinkman, 2002: 69).

BATRACHOSAUROIDIDAE Auffenberg, 1958
Gen. et sp. indet.
(Fig. 7C)

Locality—USNM Loc. 42183.

Material—Five dorsal vertebral centra.

Description—The articular faces of these hourglass-shaped centra bear ossified cartilage caps. The ends are slightly amphicoelous, with a very shallow central depression. These features are consistent with assignment to Batrachosauroididae (Estes, 1969a), although the present specimens are much smaller than those from younger beds.

URODELA indet.

Localities—USNM Locs. 42175, 42183, 42222; YPM Loc. 63-19.

Material—Three partial dentaries, two partial maxillae, one partial dentary/maxilla, 16 atlantes, 11 vertebral centra, three ilia, one humerus(?).

Description—Numerous specimens derive from urodele amphibians but are too incomplete for more specific assignment. Most vertebral centra are worn, but many are deeply amphicoelous and lack evidence of calcified cartilage on the articu-
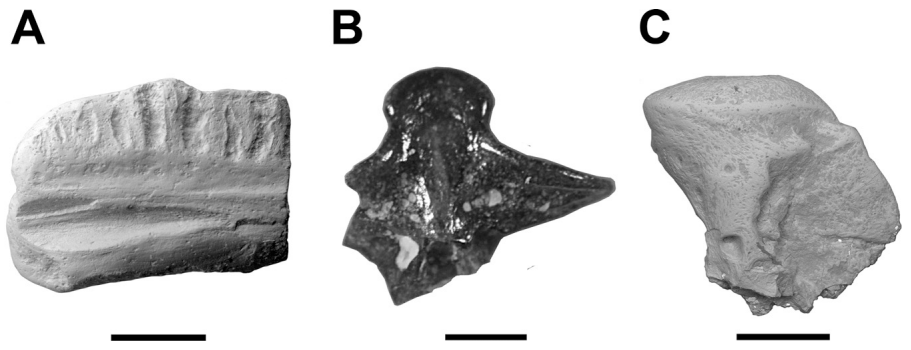
FIGURE 7. Urodeles from the Cloverly Formation. **A**, USNM 546516, cf. Scapherpetontidae, left dentary fragment, medial view; **B**, USNM 546519, cf. Scapherpetontidae, atlas, ventral view; **C**, USNM 546822, Batrachosauroididae indet., incomplete vertebra, ventral view. Scale bars equal 1 mm (**A**, **C**) and 0.5 mm (**B**).

lar ends that would suggest batrachosauroidid affinities (Fig. 7C). Six trunk vertebrae from USNM Loc. 42222 resemble those of *Opisthotriton* in having medially compressed centra and transverse processes with straight anterior margins and anteriorly angled posterior margins in dorsal view, but they do not preserve diagnostic features of that taxon.

ANURA Fischer von Waldheim, 1813
SCOTIOPHRYNE Estes, 1969b
cf. *SCOTIOPHRYNE* sp.
(Fig. 8A, B)

Localities—USNM Locs. 42183, 42222.
Material—One partial maxilla, five indeterminate skull elements.

Description—These cranial elements have high-relief, pustular ornament that is most similar to *Scotiophryne pustulosa* from the Maastrichtian Hell Creek Formation (Estes, 1969b). The maxilla (USNM 546685) is similar in size to that form and considerably larger than those recovered for other Cloverly anurans. The maxilla bears a dorsoventrally tall anterior section (Fig. 8A, B). Although the ornament of *S. pustulosa* is diagnostic (Estes, 1969b; Gardner, 2008), we are reluctant to refer these fragmentary materials to a Maastrichtian taxon. Unfortunately, the taxonomic position of *Scotiophryne* is uncertain, and we cannot yet suggest a higher-level assignment within Anura for these specimens.

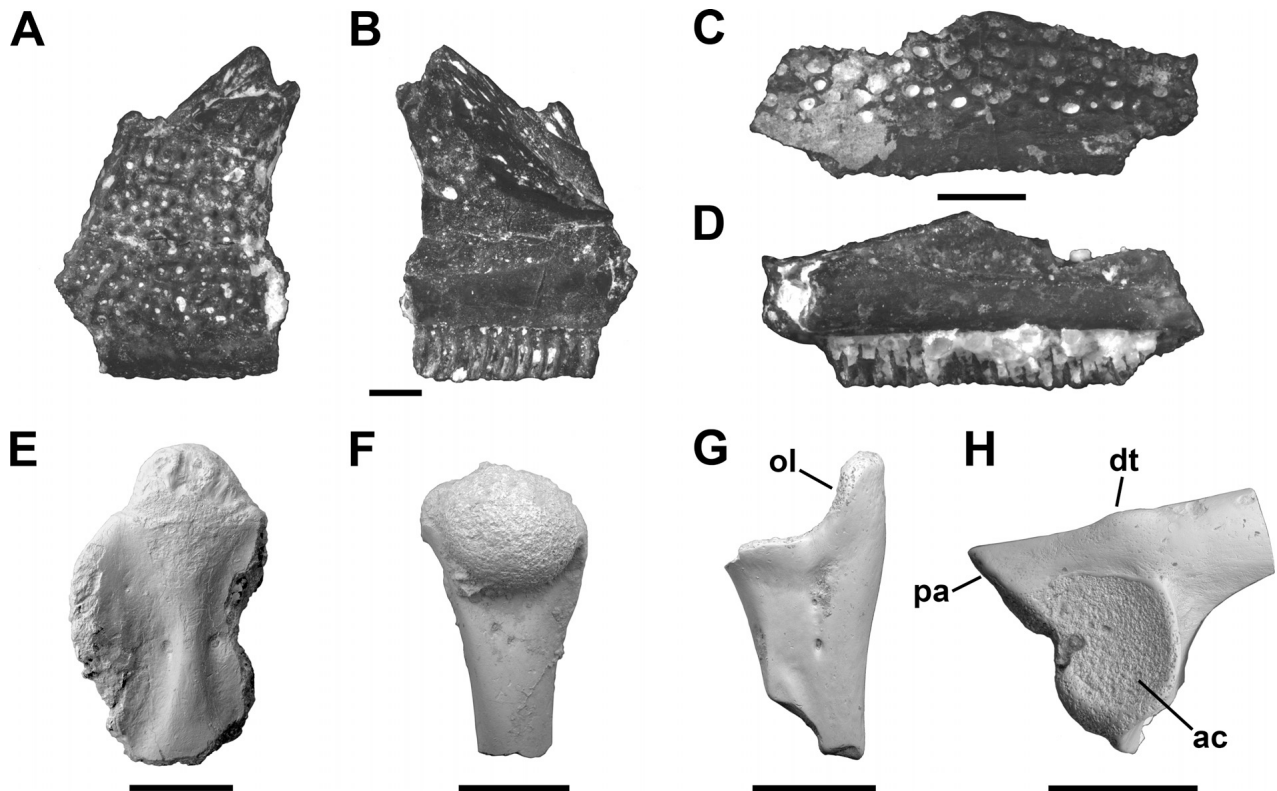ANURA indet., species A
(Fig. 8C, D)

FIGURE 8. Anurans from the Cloverly Formation. **A**, USNM 546685, cf. *Scotiophryne* sp., left maxilla fragment, lateral view; **B**, USNM 546685, left maxilla fragment, medial view; **C**, USNM 546686, Anura 'species A,' partial right maxilla, lateral view; **D**, USNM 546686, Anura 'species A,' partial right maxilla, medial view; **E**, USNM 546520, Anura indet., vertebra, dorsal view; **F**, USNM 546687, Anura indet., distal right humerus, ventral view; **G**, USNM 546521, Anura indet., proximal radioulna, medial or lateral view; **H**, USNM 546522, Anura indet., acetabular part of right ilium, lateral view. **Abbreviations**: **ac**, acetabulum; **dt**, dorsal tubercle; **ol**, olecranon; **pa**, pars ascendens. Scale bars equal 1 mm.

Localities—USNM Locs. 42175, 42183, 42222, 43420.

Material—16 partial maxillae, two partial dentaries, four indeterminate jaw fragments, 49 indeterminate skull elements.

Description—'Species A' is distinguished by its low-relief, pitted cranial ornament. The maxillae possess a supradental shelf and coarse, almost pustular (Estes, 1969b) sculpturing on the lateral surface (Fig. 8C, D). The teeth are small, pleurodont, pedicellate, and tightly associated.

ANURA indet.
(Fig. 8E–H)

Localities—USNM Locs. 42175, 42183, 42222, 43420.

Material—Six skull elements, 31 vertebral centra (eight missing the condyles), one posterior dorsal centrum, four partial ilia, 11 partial humeri, 10 radioulnae, four partial distal limbs.

Description—Anuran skull elements are identified based on their distinctive surface texture. Where preserved, the teeth are pedicellate and largely homodont. The vertebral centra are dorsoventrally compressed and often possess well-developed anterior articular condyles (cf. Brinkman, 2002:73). They can be differentiated from those of other amphibians by their compact shape in dorsal view and broad transverse processes (Fig. 8E). The humeri have a distinct distal articular ball and a flattened area on the crista medialis (Fig. 8F; cf. Estes, 1969b:figs. 3, 4; Estes and Sanchíz, 1982:fig. 10), and may represent multiple taxa. Anuran radii and ulnae are fused, forming a single, double-shafted radioulna that bears a strongly concave olecranon (Fig. 8G). The ilia are typically anuran; one example shows a robust pars ascendens and a reduced dorsal tubercle (Fig. 8H).

LISSAMPHIBIA indet.

Localities—USNM Locs. 42175, 42183, 42146, 42222; YPM 63–19.

Material—160 jaw fragments, eight skull fragments, three atlantes, four vertebral centra, 168 partial vertebrae, 12 partial limbs.

Description—A variety of poorly preserved fragments are referred to Lissamphibia based on general similarities with elements of known fossil forms (predominately urodeles and albanerpetontids), despite our inability to assign them to lower-level taxa. These include dentigerous elements with pleurodont implantation and narrow, straight-edged tooth bays, as well as fragments of amphicoelous, hourglass-shaped vertebral centra.

REPTILIA Linnaeus, 1758
TESTUDINATA Klein, 1751
SOLEMYDIDAE Lapparent de Broin and Murelaga, 1996
NAOMICHELYS Hay, 1908
NAOMICHELYS SPECIOSA Hay, 1908
(Fig. 9A)

Localities—USNM Locs. 42175, 42179, 42183, 42222, 43420, 42244, 43632, 43638.

Material—227 carapace/plastron fragments, one hypoplastron edge, one hyo- or hypoplastron, two peripherals, one partial xiphiplastron(?), one left epiplastron, and 112 loose pustules.

Description—*Naomichelys* shell material exhibits a characteristic ornament composed of densely arranged, cylindrical tubercles or pustules. These tubercles are flattened, 0.5–1.2 mm in diameter, and have constricted bases. Most plastron specimens are fragmentary, but a nearly complete left epiplastron (USNM 546760; preserved length = 115 mm; Fig. 9A) shows ornament extending around the lateral margin and narrow anteroposterior sulci on its interior surface.

PLEUROSTERNIDAE Cope, 1868
?GLYPTOPSINAE (Marsh, 1890a)
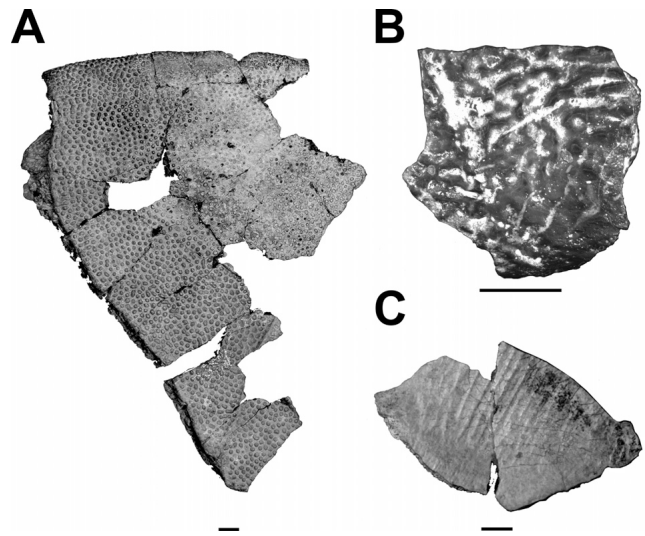"*GLYPTOPS*" *PERVICAX* Hay, 1908
(Fig. 9B)

FIGURE 9. Turtles from the Cloverly Formation. **A**, USNM 546760, *Naomichelys speciosa*, left epiplastron, ventral/external view; **B**, USNM 546709, "*Glyptops*" *pervicax*, carapace fragment, external view; **C**, USNM 546762, Testudinata indet., shell fragment, external? view. Scale bars equal 5 mm.

Localities—USNM Locs. 42175, 42179, 42183, 42146, 42222, 43422, 42244, 43627, 43628, 43629, 43632, 43635, 43638; YPM 63-19.

Material—152 carapace/plastron fragments, four hyo- or hypoplastra, one neural, 11 peripherals, two pleurals.

Description—These specimens have a faint, winding sculpture composed of low-relief, convoluting ridges (Fig. 9B), resembling that on *Glyptops plicatulus* and specimens previously assigned to "*G.*" *pervicax* (Ostrom, 1970). The exterior sculpture wraps around the edges of the peripherals, and these marginal pieces show that the carapace narrows to a rounded-edged shelf. The largest of these (USNM 546765), 5.5 cm long and 3.2 cm wide, narrows from almost 2 cm in thickness to 5 mm at the lateral edge. None of the specimens clarify the generic assignment of "*G.*" *pervicax*, which was considered indeterminate by Gaffney (1979).

TESTUDINATA indet., species A

Localities—USNM Locs. 42179, 42183, 42146, 42244, 43628, 43632, 43638.

Material—32 indeterminate carapace/plastron fragments, four carapace fragments, five peripherals, one pleural.

Description—These shell fragments differ from *Naomichelys* and "*G.*" *pervicax* in having a smooth exterior surface lacking any ornamentation. The largest specimen (USNM 546761), a 5.2-cm-long carapace fragment, is quite thin (1–5 mm) and slightly curved. Although Ostrom (1970) identified two additional turtles in the Cloverly Formation based on humeri, they cannot be compared with the present materials representing 'species A.'

TESTUDINATA indet.
(Fig. 9C)

Localities—USNM Locs. 42161, 42175, 42179, 42183, 42146, 42222, 42244, 43627, 43628, 43629, 43632, 43635, 43636, 43637, 43638.

Material—222 indeterminate carapace/plastron fragments, two neurals, 10 peripherals, three pleurals, two plastron fragments,

four carapace/plastron fragments with pitted ornament, one carapace/plastron fragment with long ridges, one ilium.

Description—A cross-sectional diploë structure characterizes turtle carapace and plastron fragments, certain of which exhibit distinctive surface features, including one from USNM Loc. 42183 with parallel, laterally oriented, dorsal ridges. Two possibly diagnostic ornamentations are observed on specimens from USNM Loc. 43638, one characterized by long, irregular ridges (Fig. 9C) and another by small, irregular pits (~0.5 mm in diameter). An ilium from USNM Loc. 42244 (USNM 546451) represents one of the stratigraphically lowest vertebrates recovered from the formation.

SQUAMATA Oppel, 1811
SCINCOMORPHA Camp, 1923
PARAMACELLODIDAE Estes, 1983
PARAMACELLODUS Hoffstetter, 1967
PARAMACELLODUS KEEBLERI Nydam and Cifelli, 2002
(Fig. 10A)

Locality—USNM Loc. 42183.
Material—One partial left dentary.
Description—The three preserved teeth on this specimen (USNM 546523; Fig. 10A) show two features of *P. keebleri*: narrow, tall proportions with well-developed anterior and posterior apical cuspules separated by a 'step,' and a medially offset anterior carina (Nydam and Cifelli, 2002). This offset makes the teeth appear slightly rotated in occlusal view. Both anterior and poste-

rior carinae are well developed, but the posterior is longer, resulting in posteriorly located apices that give a falsely recurved appearance (sensu Nydam and Cifelli, 2002). The supradental shelf is robust. The largest tooth is ca. 2.5 mm tall.

PARAMACELLODIDAE? indet., species A
(Fig. 10B)

Locality—USNM Loc. 42183.
Material—Two indeterminate jaw fragments, each bearing a single tooth.
Description—The two teeth are proportionally very wide: the better-preserved tooth is ca. 0.75 mm wide but only 1 mm tall, and therefore has a height:mediolateral width ratio only half that of *P. keebleri* (Fig. 10B). It also bears a short anterior carina with a slight 'step,' but unlike *P. keebleri*, the posterior carina is not much longer, and the apical cusp sits closer to the lateral midpoint (cf. Nydam and Cifelli, 2002:fig. 4A). These features suggest that it pertains to an undescribed taxon.

PARAMACELLODIDAE indet.

Locality—USNM Loc. 42222.
Material—One anterior left dentary.
Description—Although similar in size to the teeth of *P. keebleri*, the three teeth on this dentary fragment (USNM 546727) lack autapomorphies of that taxon. The crowns exhibit medial striae and rounded, nondiagnostic cusps, as well as paramacellodid synapomorphies such as medially swollen bases, a medial crown concavity, and slightly rotated cusps (Nydam and Cifelli, 2002). The unusual placement of a central tooth medially in front of the other two may be pathological.

TEIIDAE Gray, 1827
PTILOTODON Nydam and Cifelli, 2002
PTILOTODON WILSONI Nydam and Cifelli, 2002
(Fig. 10C, D)

Localities—USNM Locs. 42183, 42222.
Material—Two partial right dentaries, two partial left maxillae.
Description—The teeth in these elements exhibit apical anterior and posterior expansions characteristic of *P. wilsoni*, giving their apices a triangular appearance (Fig. 10C). The expansions are offset from the center but not developed into accessory cusps. The crowns also lack medial striae. Several subcircular resorption pits are visible. The subdental shelves are narrow, with some cementum around the tooth bases. The maxillae fragments preserve part of the lateral surfaces above the tooth row (Fig. 10D).

TEIIDAE indet., species A
(Fig. 10E)

Localities—USNM Locs. 42183, 42222.
Material—Two partial right maxillae, one partial dentary.
Description—The tapered tooth crowns on these specimens have very narrow, posteriorly oriented cusps, giving the teeth a conical appearance (Fig. 10E). The tooth bases bear cementum, and USNM 546524, which preserves one complete tooth and the bases of two others, exhibits subcircular resorption pits located centrally at the base of each tooth. The cusps differ from those of *P. wilsoni*, indicating the presence of a second teiid species.

TEIIDAE indet.

Locality—USNM Loc. 42183.
Material—Four indeterminate jaw elements.
Description—The slender, tapered tooth crowns in these jaw fragments have apices bearing moderately thin, posteriorly oriented cusps. Unlike paramacellodid teeth, those of teiids are more delicate and exhibit a stronger posterior curvature. The small anteroposterior crown expansions reported in some teiids (Nydam, 2002) are not observed on the Cloverly specimens.
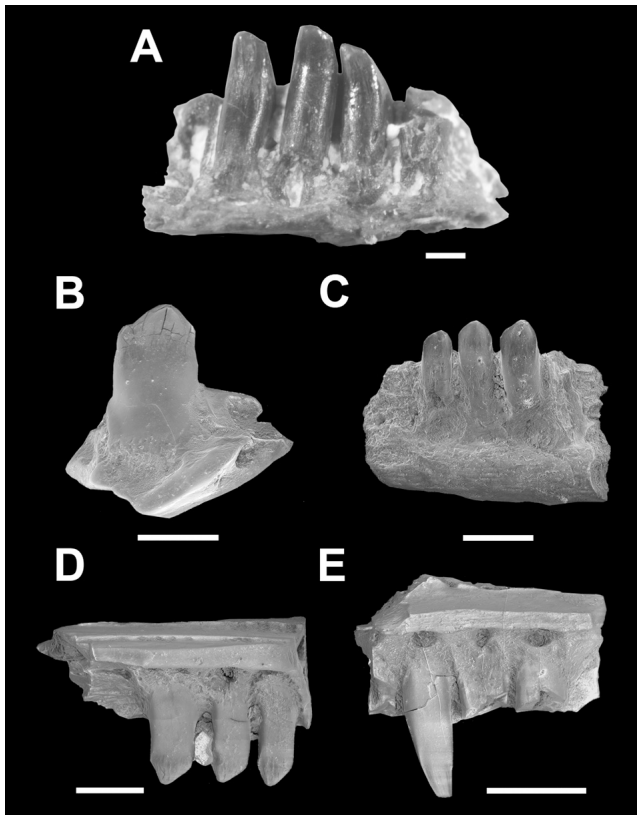

FIGURE 10. Lizards from the Cloverly Formation. **A**, USNM 546523, *Paramacellodus keebleri*, left dentary? fragment, medial view; **B**, USNM 546525, Paramacellodidae 'species A,' tooth, lingual view; **C**, USNM 546688, *Ptilotodon wilsoni*, right dentary fragment, medial view; **D**, USNM 546526, *Ptilotodon wilsoni*, left maxilla fragment, medial view; **E**, USNM 546524, Teiidae 'species A,' right maxilla fragment, medial view. Scale bars equal 0.5 mm.

However, other characteristic teiid features, including thick cementum around tooth bases, deep, subcircular resorption pits (Nydam and Cifelli, 2002), and a wide sulcus dentalis (Cifelli et al., 1999), are observed to varying degrees.

SQUAMATA indet.

Localities—USNM Locs. 42175, 42183, 42222.

Material—Five partial dentaries, two partial maxillae, 17 partial jaw elements.

Description—These squamate jaw fragments lack preserved teeth or have weathered or otherwise nondiagnostic tooth crowns, and therefore cannot be assigned to a lower taxonomic group. They can be assigned to Squamata based on the presence of one or more of the following: robust teeth and broad sub- or supradental shelves (unlike amphibians), thick cementum around tooth bases, medially curved teeth, and deep resorption pits.

ARCHOSAURIA Cope, 1870
CROCODYLIFORMES Hay, 1930
NEOSUCHIA Benton and Clark, 1988

Comment—Below we describe a large sample of crocodyliform teeth and compare them with those of four known Early Cretaceous groups. At present, these comparisons should be considered tentative, and we are in the process of a more detailed morphometric study of these teeth to better determine how many taxonomic entities may be represented.

cf. BERNISSARTIDAE Dollo, 1883
Gen. et sp. indet.
(Fig. 11A, B)

Localities—USNM Locs. 42175, 42183, 42222, 43420.

Material—50 acuminate teeth and partial teeth, 64 'molariform' teeth.

Description—Bernissartid-like teeth are typically small, 1–2 mm wide mesiodistally and 1–2 mm tall. They are often labiolingually compressed and kidney-shaped in occlusal view (Fig. 11A). Most have rounded but slightly acuminate crowns, a constriction just above the root, and an elliptical apical wear facet. The broad mesial and distal margins lack well-developed carinae, and the labial and lingual faces are slightly convex with

apicobasally directed striae that converge apically (Fig. 11B; cf. Schwarz-Wings et al., 2009). The two faces are subequal in area. Mesiodistally expanded 'molariform' teeth are also present and may pertain to this group.

cf. ATOPOSAURIDAE Gervais, 1871
Gen. et sp. indet.
(Fig. 11C, D)

Localities—USNM Locs. 42175, 42183, 42146, 42222, 43420, 43422.

Material—865 teeth and partial teeth, 102 'molariform' teeth, 41 'long' teeth.

Description—Teeth comparable to those of atoposaurids are common. The crenulated carinae seen in *Theriosuchus* (e.g., Buscalioni et al., 2008; Schwarz-Wings et al., 2009) are not as pronounced on Cloverly specimens, but these teeth bear other *Theriosuchus*-like features such as a labiolingually compressed crown (Fig. 11C), a constriction near the crown base, and marked mesial and distal carinae. They are triangular and small (maximum height and width, 4.5 mm × 2 mm), with varying degrees of recurvature. Most have a convex labial face and a slightly concave lingual face, and some show partially anastomosing striae; those nearest the tooth center in lingual view are vertically oriented, fanning out mesially and distally (Fig. 11D). Atoposaurid-like 'molariform' teeth have lower, mesiodistally broad crowns, a weak basal constriction, and more evenly spaced striae. Unlike bernissartid teeth, the lingual surface area is smaller than the labial. More acuminate teeth have proportionally taller crowns (1.5–5 mm) with a height:width ratio of at least 4:1. The carinae enclose a smaller, but more strongly concave, lingual surface area. Atoposaurids also exhibit reduced or absent dermal armor (Buscalioni and Sanz, 1988), so the abundant dermal scutes in our samples likely derive from other crocodyliform taxa.

cf. GONIOPHOLIDIDAE Cope, 1875
Gen. et sp. indet.
(Fig. 11E)

Localities—USNM Locs. 42159, 42175, 42183, 42222, 43420.
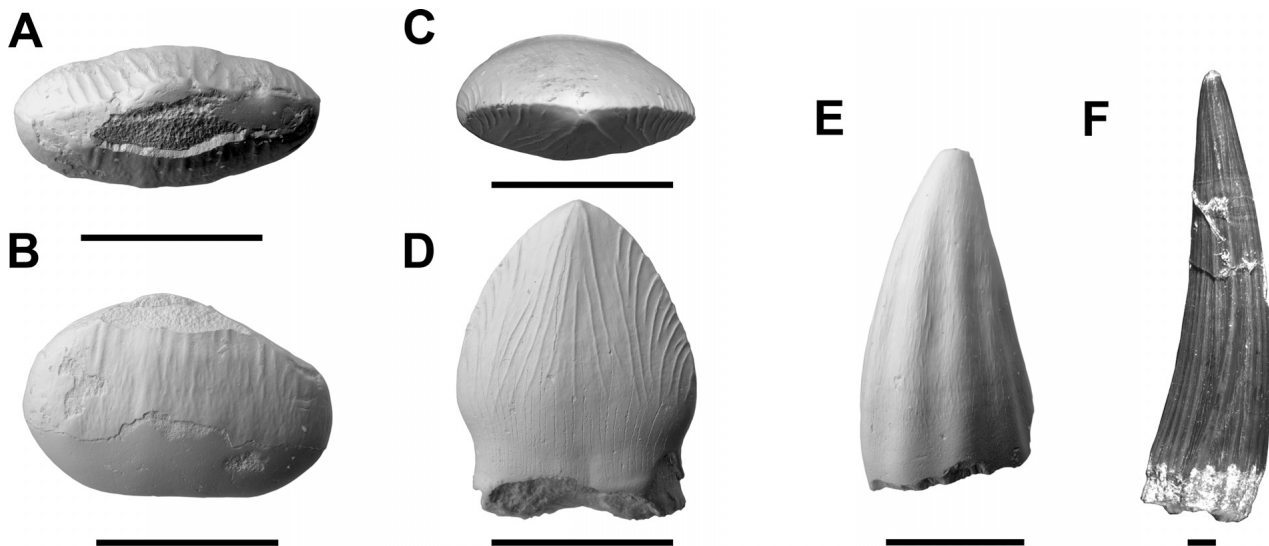**Material**—39 teeth and partial teeth.

FIGURE 11. Crocodylian teeth from the Cloverly Formation. **A**, USNM 546838, cf. Bernissartidae, occlusal view; **B**, USNM 546838, cf. Bernissartidae, labial view; **C**, USNM 546839, cf. Atoposauridae, occlusal view; **D**, USNM 546839, cf. Atoposauridae, lingual view; **E**, USNM 546837, cf. Goniopholididae, labial view; **F**, USNM 546836, cf. Pholidosauridae, mesiodistal view. Scale bars equal 1 mm.

Description—Teeth exhibiting only slight labiolingual compression, nearly circular bases, weakly developed mesial and distal carinae, and relatively few radiating ridges are comparable to those of goniopholidids (Fig. 11E). *Goniopholis* teeth possess six or more shallow, radiating ridges extending from the apex (Buscalioni et al., 2008; Schwarz-Wings et al., 2009). Larger crowns often have rounded apices and a low height:width ratio (2:1). Some specimens exhibit slight lingual curvature and wrinkled striae. Ostrom (1970) questioned whether the larger, finely striated Cloverly crocodylian teeth belong to *Goniopholis*; similar teeth recovered during this study are compared here with those of pholidosaurids (see below).

cf. PHOLIDOSAURIDAE Zittel and Eastman, 1902
Gen. et sp. indet.
(Fig. 11F)

Localities—USNM Locs. 42175, 42179, 42183, 42222, 43416, 42244, 43632.
Material—503 teeth and partial teeth.
Description—Numerous large, conical teeth resemble those of extant crocodylians and are here compared with Pholidosauridae (cf. Bonde, 2004). These teeth exhibit variation consistent with the heterodonty noted in pholidosaurids (Estes and Sanchíz, 1982). All teeth bear carinae and longitudinal ridges, but some crowns are slender with fine striations (Fig. 11F), whereas others are stouter with coarser striations and rounded apices. The largest specimen (USNM 546840) is 23 mm tall, although still incomplete. Most large Cloverly crocodylian teeth fit the description above, including those previously described as being similar to *Alligator* (Ostrom, 1970). Seventeen 'molariform' teeth (42183) are currently referred to Crocodyliformes (see below) but might represent posterior pholidosaurid teeth.

CROCODYLIFORMES indet.

Localities—USNM Locs. 42175, 42179, 42183, 42222, 43418, 43420, 43422, 42244, 42245, 43629, 43632.
Material—One left dentary, 418 isolated teeth, 17 'molariform' teeth and partial teeth, 119 partial osteoderms, two cervical vertebrae, eight dorsal vertebral centra, two proximal right femora, one distal right femur, one metatarsal, one ungual.
Description—Crocodyliform teeth are among the most common Cloverly vertebrate fossils; some are distinctive enough to suggest the above comparisons, but many are morphologically intermediate. The dermal bones and scutes bear irregularly spaced, rounded pits of varying size and shape (e.g., Bonde, 2004). The cervical vertebrae have low-set parapophyses, and dorsal vertebrae are weakly amphicoelous. Most centra derive from subadult individuals, having separated along the neurocentral sutures (Brochu, 1996). The proximal right femur (USNM 546766) has a lobate, anteriorly flat head that is slightly medially offset, a proximally placed, ridge-like fourth trochanter, and a very narrow greater trochanter. An associated distal section bears asymmetric lateral and medial condyles separated by a shallow intercondylar fossa. The fragmentary ungual is acuminate and nearly straight, with a flat ventral surface, a highly arched dorsal surface, and grooves on the lateral sides.

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
Gen. et sp. indet.

Localities—USNM Locs. 42175, 42183, 42222.
Material—Nine partial teeth.
Description—These specimens are referred to Tetanurae based on the presence of 'enamel wrinkles' (Brusatte et al., 2007) as well as serration size and density (2–2.4 per millimeter for both

anterior and posterior serrations; Ostrom, 1969). The largest fragment is a crown base (USNM 546473) with a basal length of almost 2 cm and a width of 1.1 cm. These teeth are strongly laterally compressed, unlike the more robust condition of most tyrannosauroids. They could belong to *Acrocanthosaurus*, now known from the Cloverly (D'Emic et al., 2011), but do not preserve diagnostic features of that taxon.

DROMAEOSAURIDAE Matthew and Brown, 1922
DEINONYCHUS Ostrom, 1969
DEINONYCHUS ANTIRRHOPUS Ostrom, 1969
(Fig. 12A)

Localities—USNM Locs. 42175, 42183, 42222, 42233 42245, 43632.
Material—129 teeth and partial teeth, one right pedal phalanx III-3, on left pedal phalanx IV-3/4, one left pedal phalanx IV-1.
Description—Teeth referred to *D. antirrhopus* correspond to those described by Ostrom (1969) in size and shape (Fig. 12A). Incomplete specimens are referred based on serration size, shape, and density per millimeter (3.5 posteriorly and 5.0 anteriorly). The pedal phalanx III-1 (USNM 546470) is 4.9 cm long, and closely resembles the corresponding element from the holotype (YPM 5205).

OVIRAPTOROSAURIA Barsbold, 1976
MICROVENATOR Ostrom, 1970
MICROVENATOR CELER Ostrom, 1970

Locality—USNM Loc. 42179.
Material—One middle cervical vertebra.
Description—A single, slightly deformed vertebra (USNM 546292) is referred to this taxon. Although larger than the presumably juvenile holotype (AMNH 3041), this specimen bears numerous similarities with *Chirostenotes* that suggest referral to a caenagnathid theropod. These include triangular, anteroventrally facing parapophyses, two slit-like pneumatic foramina within fossae on the lateral centrum surface, deep anterior peduncular fossae, a transverse process with a triangular cross-section, and no infradiapophyseal fossa (Sues, 1997).

THEROPODA indet., species A
(Fig. 12B)

Localities—USNM Locs. 42183, 42222, 43420.
Material—38 teeth and partial teeth.
Description—Teeth of 'species A' are weakly recurved, with small serrations on both carinae (Fig. 12B). The posterior serrations (6/mm) are larger than the anterior ones (8/mm), but both sets are significantly smaller than those of *D. antirrhopus*. The teeth are also proportionally tall relative to their width: one relatively complete specimen (USNM 546763) is 9 mm tall with a basal width of 4 mm. These teeth resemble those of *Richardoestesia* more than those of troodontids, dromaeosaurids, or tyrannosauroids. Several very small specimens lack serrations entirely, which we interpret as a juvenile feature.

THEROPODA indet., species B
(Fig. 12C)

Localities—USNM Locs. 42183, 42222.
Material—Six teeth and partial teeth.
Description—Tooth crowns of 'species B' range from 1 to 5 mm in height and 1 to 4 mm in basal length. Both anterior and posterior carinae are serrated, although the anterior serrations (17/mm) are much smaller than the posterior serrations (8/mm) (Fig. 12C). The anterior edge curves posteriorly, with an abrupt increase in curvature near the crown mid-height. The posterior edge is only slightly concave in lateral view. The teeth resemble those of some troodontids, particularly in the discrepancy in serration size between the anterior and posterior carinae.
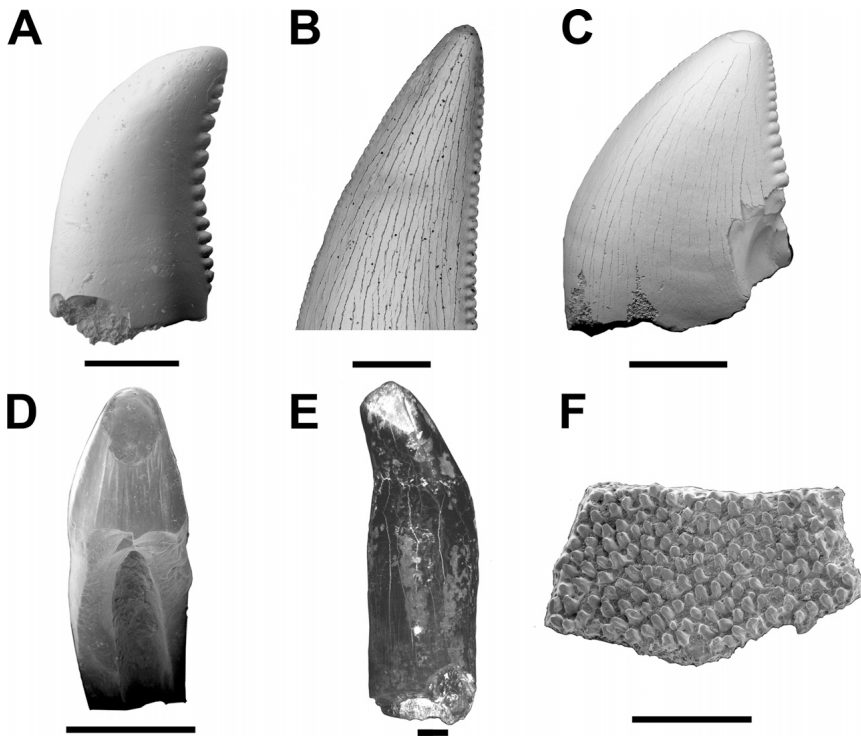
FIGURE 12. Saurischian dinosaurs from the Cloverly Formation. **A**, USNM 546707, *Deinonychus antirrhopus*, tooth, labiolingual view; **B**, USNM 546763, Theropoda 'species A,' tooth apex, labiolingual view; **C**, USNM 546699, Theropoda 'species B,' tooth, labiolingual view; **D**, USNM 546469, ?Aves indet., tooth, lingual view; **E**, USNM 546527, Titanosauriformes indet., tooth, mesiodistal view; **F**, USNM 546652, ?sauropod eggshell, external view. Scale bars equal 1 mm (**A–D**, **F**) and 2 mm (**E**).

THEROPODA indet.

Localities—USNM Locs. 42159, 42175, 42179, 42183, 42222, 42244, 43628.

Material—115 teeth and partial teeth, one metapodial, one metatarsal, 19 partial limb elements, three pedal IV phalanges, five unguals.

Description—Numerous fragmentary specimens can be identified only as indeterminate theropod. The mostly fragmentary teeth are laterally compressed and recurved, with serrated carinae, and smooth enameled surfaces. Other specimens include large, hollow limb sections, such as a 9-cm-long section of ?tibia (USNM 546253) and a metapodial (USNM 546478). The pedal phalanges are proportionally short, indicating derivation from digit IV. The largest (USNM 546477) is 3.2 cm long; the smallest (USNM 546475) has a dorsoventral height (8 mm) greater than its anteroposterior length (7 mm). All of the unguals are small (≤3 mm long), dorsoventrally curved, and bear concave articular surfaces. Two show mediolateral surface grooves. They possibly derive from the manus, and may belong to a coelurosaur, but their articular surfaces differ from those of *Microvenator celer* (Ostrom, 1970:pl. 12P). Ostrom (1970) tentatively referred several theropod postcranial specimens from the Cloverly to Megalosauridae, and compared them with *Allosaurus*, but none of the present materials exhibit synapomorphies of particular theropod clades. Nonetheless, they support the presence of a large theropod in the Cloverly fauna.

?AVES Linnaeus, 1758
Gen. et sp. indet.
(Fig. 12D)

Localities—USNM Locs. 42175, 42183, 42222.

Material—Three teeth, three partial metatarsals(?).

Description—These teeth are laterally compressed and triangular in profile, lacking strong recurvature. The carinae lack serrations. The single specimen retaining a root (USNM 546469) shows a very slight constriction just below the crown base (Fig. 12D). Three fragmentary specimens resemble the distal articular condyles of avian tarsometatarsals in exhibiting a strongly curved projection with a well-finished articular surface.

SAUROPODA Marsh, 1878b
TITANOSAURIFORMES Salgado, Coria, and Calvo, 1997
Gen. et sp. indet.
(Fig. 12E, F)

Localities—USNM Locs. 42159, 42175, 42179, 42183, 42222, 43418, 43422, 43632.

Material—255 teeth and partial teeth, 14 teeth/partial teeth with poorly developed carinae, one caudal vertebra.

Description—Sauropod teeth and tooth fragments are identified based on their unstriated enamel, circular cross-section, and cylindrical base; well-preserved specimens show a wrinkled enamel texture (Wilson and Sereno, 1998; Fig. 12E). They resemble the teeth of titanosauriforms generally. Ostrom (1970:83) compared similar teeth with *Astrodon* and *Pleurocoelus*, but these cannot be confidently assigned to those genera or to the Cloverly forms *Rugocaudia* or *Sauroposeidon* (D'Emic and Foreman, 2012; Woodruff, 2012). At two sites (USNM Locs. 42183, 42222), well-worn teeth are preserved with a polished outer surface and rounded, mesiodistal ridges that run longitudinally from apex to base. Dorsal and caudal vertebrae, ribs, scapulae, humeri, and other long bone pieces occur commonly in Cloverly sediments and provide further evidence for the abundance of sauropods, although most are poorly preserved. Rare eggshell fragments typically show a mammillary surface morphology characteristic of titanosaur eggs (Fig. 12F).

ORNITHISCHIA Seeley, 1887
ORNITHOPODA Marsh, 1881
ZEPHYROSAURUS Sues, 1980
cf. *ZEPHYROSAURUS* sp.
(Fig. 13A)

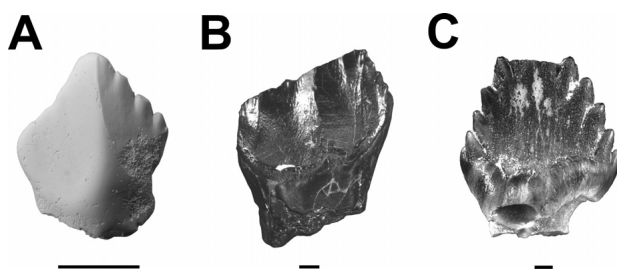**Localities**—USNM Locs. 42175, 42183, 42222.

FIGURE 13. Ornithischian dinosaur teeth from the Cloverly Formation. **A**, USNM 546668, cf. *Zephyrosaurus* sp., maxillary or posterior dentary tooth, labiolingual view; **B**, USNM 546661 *Tenontosaurus tilletti*, maxillary or posterior dentary tooth, labiolingual view; **C**, USNM 546662, *Sauropelta edwardsi*, maxillary or posterior dentary tooth, labiolingual view. Scale bars equal 1 mm.

Material—11 premaxillary(?) teeth, one maxillary or posterior dentary tooth.

Description—These putative premaxillary teeth have constricted roots, a bulbous shape in lateral view, and pointed apices that curve slightly anteriorly. They are rounded in occlusal view and resemble the premaxillary teeth of other 'hypsilophodontian'-grade ornithopods such as *Thescelosaurus* and *Orodromeus*. We compare them with *Zephyrosaurus* as the sole known Cloverly form with this morphology; *Tenontosaurus* lacks premaxillary teeth (Ostrom, 1970). A single, triangular maxillary or posterior dentary tooth bearing a small number of cusps is typical for basal euornithopods (Fig. 13A) and is also referred to this taxon.

IGUANODONTIA Baur, 1891 (non Dollo, 1888)
TENONTOSAURUS Ostrom, 1970
TENONTOSAURUS TILLETTI Ostrom, 1970
(Fig. 13B)

Localities—USNM Locs. 42175, 42183, 42245, 43638.
Material—17 teeth, one anterior dorsal vertebra, one indeterminate caudal vertebra.
Description—Teeth assigned to *Tenontosaurus* show minimal basal constriction and several evenly spaced, vertical, labial ridges on either side of a pronounced central ridge (Fig. 13B). Denticles cover the mesial and distal edges except in heavily worn specimens; these are considerably finer than those found on teeth belonging to ankylosaurs (Ostrom, 1970:pl. 17). Vertebral centra are amphiplatyan with 'weakly heart-shaped' (Forster, 1990) faces in anterior and posterior view, are proportionally short, and bear straight ventral keels. Zygapophyseal facets are heavily worn but appear to incline about 45° (Ostrom, 1970). A weak, 4-mm-wide indentation occurs between the facets and runs anteroposteriorly across the dorsal surface on the more anterior vertebra (USNM 546258). This indentation is significantly wider (about 1 cm) on the indeterminate caudal vertebra (USNM 546433), on which the anterior articular surface is larger than the posterior. The indentation widens anteriorly and posteriorly on both specimens, given the rounded cross-sectional shape of the zygapophyses.

ANKYLOSAURIA Osborn, 1923
NODOSAURIDAE Marsh, 1890b
SAUROPELTA Ostrom, 1970
SAUROPELTA EDWARDSI Ostrom, 1970
(Fig. 13C)

Localities—USNM Locs. 42183, 42222.
Material—12 teeth.

Description—As in most nodosaurids, the *Sauropelta* teeth are broadly triangular in lateral view, with large denticles adorning the primary ridge (Fig. 13C). This ridge is faintly sinusoidal in occlusal view, and the teeth are laterally compressed, with an enlarged basal cingulum. Most are weathered and have smooth labial and lingual surfaces, although one shows ridges on the lingual crown face (USNM 546726). The most complete tooth preserves nine denticles (USNM 546662); two additional denticles are missing at the apex. The teeth differ from the single described tooth of *Tatankacephalus* (Parsons and Parsons, 2009) in bearing asymmetrically arranged denticles across the primary ridge.

ANKYLOSAURIA indet.

Localities—USNM Locs. 42179, 42183, 42222, 42350, 42244, 43632, 43636.
Material—Seven partial teeth, 46 osteoderm fragments, one partial plate-like osteoderm, six associated partial dorsal, sacral, and caudal vertebrae.
Description—Despite preserving partial crowns, these tooth fragments can only be referred to Ankylosauria given their state of preservation. Weak basal crown constriction preserved in certain specimens differs slightly from that in the described teeth of the two currently known Cloverly ankylosaurs. The largest osteoderm fragment (USNM 546769) measures 5.3 cm × 5.1 cm and appears to be a quarter section of a round or diamond-shaped plate (cf. Ostrom, 1970:pl. 27). It is slightly convex, with porous bone on its ventral surface and a dorsoventrally rounded distal margin. None of the dermal bone fragments preserve apomorphies specific to an individual taxon, and might relate to either of the two ankylosaurs. Several associated but poorly preserved vertebrae were found in a bed rich in plant debris, including portions of three dorsal, one sacral, and one anterior caudal vertebrae (USNM 546291), consistent in size and preservation with the remains of a single individual.

ORNITHISCHIA indet.

Localities—USNM Locs. 42161, 42175, 42179, 42183, 42146, 42222, 43418, 43422, 42244, 43627, 43632, 43634, 43638.
Material—481 partial ossified tendons, 14 teeth and partial teeth.
Description—Ossified tendons exhibit fine linear surface striations and an elliptical cross-section. They generally lack a longitudinal groove, as would be common for most rib fragments. Because they are unknown among saurischians (and stegosaurs), we assign these specimens to Ornithischia. Incomplete or heavily worn teeth that cannot be assigned to a particular taxon with certainty are also referred here.

MAMMALIA Linnaeus, 1758
EUTRICONODONTA Kermack, Mussett, and Rigney, 1973
TRICONODONTIDAE Marsh, 1887
ALTICONODONTINAE Fox, 1976
Gen. et sp. indet.
(Fig. 14A, B)

Localities—USNM Locs. 42183, 42222.
Material—One right premolar, one upper molar, nine partial lower molars, one posterior lower molar, one edentulous posterior dentary.
Description—Alticonodontines include a number of morphologically similar Early Cretaceous taxa that are not easily distinguished based on isolated and/or fragmentary teeth, including *Jugulator*, *Corviconodon*, and *Astroconodon* (Cifelli and Madsen, 1998). These taxa tend to have deeply interlocking molars, grooves down the mesial roots, lower crown height, and well-separated cusps (Fig. 14A, B). In occlusal view, the lower molars have asymmetric cusps that are more convex labially. Multiple specimens can be assigned to this subfamily, although we are less certain of lower-level identifications because different species of
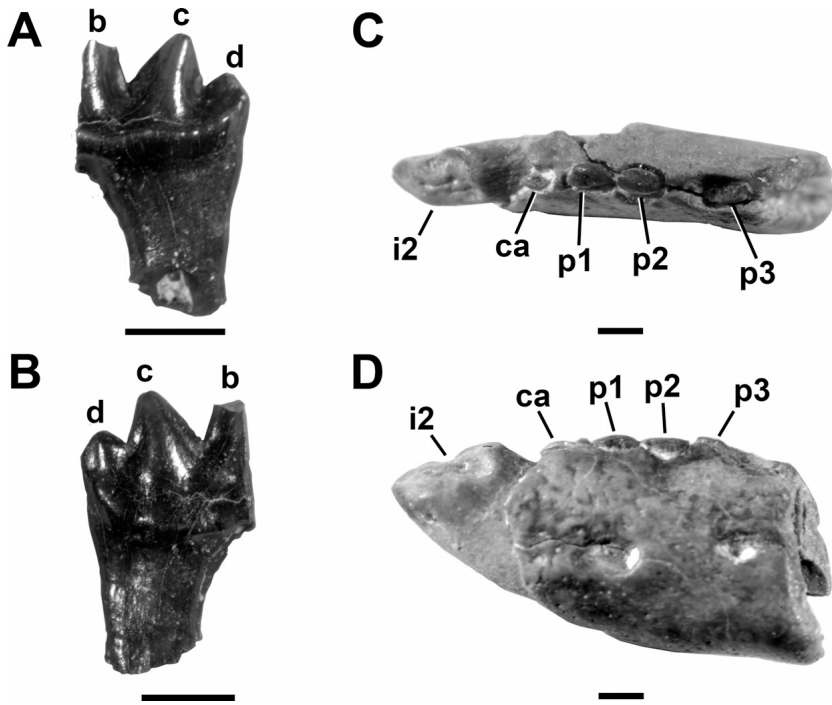
FIGURE 14. Eutriconodontan mammals from the Cloverly Formation. **A**, USNM 546689, Alticonodontinae indet., right lower molar, lingual view; **B**, USNM 546689, Alticonodontinae indet., right lower molar, labial view; **C**, USNM 546656, *Gobiconodon ostromi*, right dentary, occlusal view; **D**, USNM 546656, *Gobiconodon ostromi*, right dentary, medial view. **Abbreviations**: **b**, cusp b; **c**, cusp c; **ca**, canine; **d**, cusp d; **i2**, second incisor; **p1**, first premolar; **p2**, second premolar; **p3**, third premolar. Scale bars equal 1 mm.

the same genus are known from different formations, and may differ in size (and therefore overlap other species of closely related genera). For example, USNM 546739 is similar in size to *Corviconodon*, but shows less recumbent cusps than that genus or *Jugulator*; it is closer in morphology to *Astroconodon* but differs in size from the described species. The edentulous dentary fragment (USNM 546780), about half the size of *Corviconodon*, is tentatively assigned here based on the absence of a postdentary groove.

GOBICONODONTIDAE (Chow and Rich, 1984)
GOBICONODON Trofimov, 1978
GOBICONODON OSTROMI Jenkins and Schaff, 1988
(Fig. 14C, D)

Locality—USNM Loc. 42183.
Material—One anterior right dentary with partial i2 and roots of c, p1, p2, and p3, one isolated tooth fragment.
Description—This partial mandible (USNM 546656) preserves the lower half of a procumbent second incisor, which curves upward apically and bears a medial longitudinal groove that would have appressed the (missing) smaller first incisor (Fig. 14C, D). The roots of the canine and three premolariform teeth are visible, but in all cases breakage has occurred at the level of the dorsal alveolar margins. A vacant alveolus opens at the broken proximal end, where a deciduous tooth is known to occur (Jenkins and Schaff, 1988). The ends of all teeth are broken and subsequently heavily abraded (presumably abiotically). The anterior part of the lateral surface is broken open, exposing the long incisor root. Two dental foramina are visible on the medial surface. The mandible is relatively straight in dorsal view, with a slight medial inflection near the symphysis (Fig. 14C). The general morphology, large proportions of the incisor, and overall large size of the specimen are consistent with assignment to *G. ostromi*. It is about half the size of the holotype (MCZ 19965; Jenkins and Schaff, 1988), which suggests that it represents a juvenile.

EUTRICONODONTA indet.

Localities—USNM Locs. 42183, 42222.
Material—10 partial teeth.

Description—Several distinctive fragments of eutriconodontan molars are too incomplete for referral to a known taxon. Their sizes and morphologies do not suggest the presence of species additional to those described above.

MULTITUBERCULATA Cope, 1884
CIMOLODONTA McKenna, 1975
PARACIMEXOMYS Archibald, 1982
?*PARACIMEXOMYS* sp.
(Fig. 15A–C)

Localities—USNM Locs. 42183, 42222.
Material—One right deciduous P4, two left P2/3, one left P4, one right p4, one left m1, one right M1.
Description—*Paracimexomys* is a poorly delineated genus that has recently been redefined (Eaton and Cifelli, 2001; Kielan-Jaworowska et al., 2004), but identifying and referring isolated teeth remain problematic. Most specimens referred here are similar to ?*Paracimexomys perplexus* from the Cedar Mountain Formation (Eaton and Cifelli, 2001), but are smaller and could represent a distinct species. The left P2/3 specimens (USNM 546713, 546775) bear four cusps in two rows separated by a wide valley. The two lingual cusps are subequal in size and rounded. The posterolabial cusp is similarly sized but has a flat anterolabial face. The anterolabial cusp is the smallest, triangular, and has a flat anterolabial facet. The left P4 crown (USNM 546660) has an oblique primary row of four cusps that ascend in height toward the apex (Fig. 15A–C). Unlike in ?*P. perplexus*, these cusps are evenly spaced. The descending ridge bears four faint bulges as it approaches the basin at the posterolingual corner of the tooth. The anterolabial corner bears a single ridge-like cusp that is isolated from the main row by a notch. In occlusal view, the tooth is rectangular but more elongate than in ?*P. perplexus*. The p4 blade (USNM 546712) has relatively smooth enamel with posteriorly angled striae (six labial, five lingual) that form small cusps at the anteroposterior edge. The total preserved length (1.6 mm) represents about 3/5 of the 2.7 mm estimated total length; crown height is 1.14 mm. This suggests a smaller taxon than *Bryceomys* (Eaton, 1995) or *Cedaromys* (Eaton and Cifelli, 2001), consistent with assignment to a small species of ?*Paracimexomys*. The left
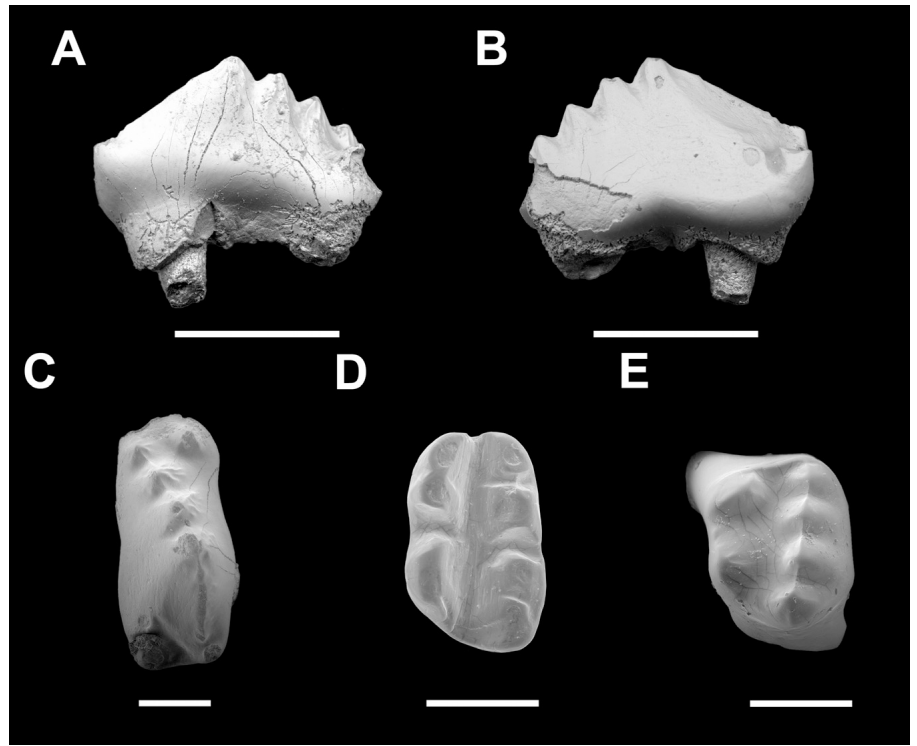
FIGURE 15. Multituberculate mammals from the Cloverly Formation. **A**, USNM 546660, ?*Paracimexomys* sp., P4, labial? view; **B**, USNM 546660, ?*Paracimexomys* sp., P4, lingual? view; **C**, USNM 546660, ?*Paracimexomys* sp., P4, occlusal view; **D**, USNM 546659, *Bryceomys* sp., right m1, occlusal view; **E**, USNM 546658, *Janumys* sp., right dP4, occlusal view. Scale bars equal 1 mm.

m1 (USNM 546773) preserves only the anterior end, with two closely approximated cusp rows that are nearly connected via a ridge. The right M1 (USNM 546772) includes about two-thirds of the tooth, with parts of four labial and two lingual cusps. The anterolabial cusp is placed nearly centrally, such that the central valley is obliquely oriented. The labial cusps are proportionally narrow labiolingually, whereas those of the lingual row are more pyramidal. The posterior cusp in this row is the largest preserved cusp.

BRYCEOMYS Eaton, 1995
BRYCEOMYS sp.
(Fig. 15D)

Locality—USNM Loc. 42183.
Material—One right m1, one partial left M2.
Description—USNM 546732 is a nearly complete lower first molar, 1.75 mm long and 1.13 mm wide. The size and proportions are quite close to both *Bryceomys intermedius* and ?*Paracimexomys perplexus* (Eaton and Cifelli, 2001), but the cusp formula of 3:4 suggests assignment to the former genus. The second upper molar (USNM 546733) is missing its anterolabial corner and posterior margin, but the anterior end of the central valley is distinctly curved and strongly resembles the condition in *B. intermedius*.

PLAGIAULACIDA Simpson, 1925
JANUMYS Eaton and Cifelli, 2001
JANUMYS sp.
(Fig. 15E)

Locality—USNM Loc. 42183.
Material—One right deciduous upper premolar.
Description—This tooth (USNM 546658) bears a lingual row of four cusps and a labial row of two (Fig. 15E). The two rows are connected via a posterior ridge and separated by a longitudinal valley. This valley opens anteriorly as well as labially between the two cusps of the labial row. The overall size and morphology are similar to teeth of *Janumys erebos* (Eaton and Cifelli, 2001).

MULTITUBERCULATA indet.

Localities—USNM Locs. 42183, 42222.
Material—Two i2, one left deciduous upper premolar, one right deciduous upper premolar, one partial P4, one partial ?m1, one partial right ?M2, one partial lower molar.
Description—These specimens include fragmentary and deciduous teeth that cannot be assigned to lower-level taxa. The i2 (USNM 546750) bears two carina that diverge from the apex and descend the labial face to converge on a basal cusp; USNM 546711 is similar but less well preserved. USNM 546771 is a six-cusped tooth that we interpret as a deciduous premolar. The cusps are arranged around the triangular perimeter of the occlusal surface, enclosing a small central basin. They vary only slightly in size but show greater differences in shape. USNM 546749 bears seven cusps, arranged similarly around a central basin. However, one cusp is absent from the perimeter, replaced by a low ridge, and an apex of the triangle of the tooth outline bears one exceptionally tiny cusp. The tooth shows greater differences in cusp shape than USNM 546771. The ?m1 fragment (USNM 546751) preserves two square cusps and the right-angled corner of the tooth. USNM 546710 preserves a single, subrectangular cusp pair separated by a narrow valley. The larger cusp is flanked anteriorly by a shelf. Its width is consistent with assignment to *Cedaromys* (Eaton and Cifelli, 2001), but it could also represent a distinct species of a related genus.

TRECHNOTHERIA McKenna, 1975
SPALACOTHERIIDAE Marsh, 1887
Gen. et sp. indet.
(Fig. 16A)

Locality—USNM Loc. 42222.
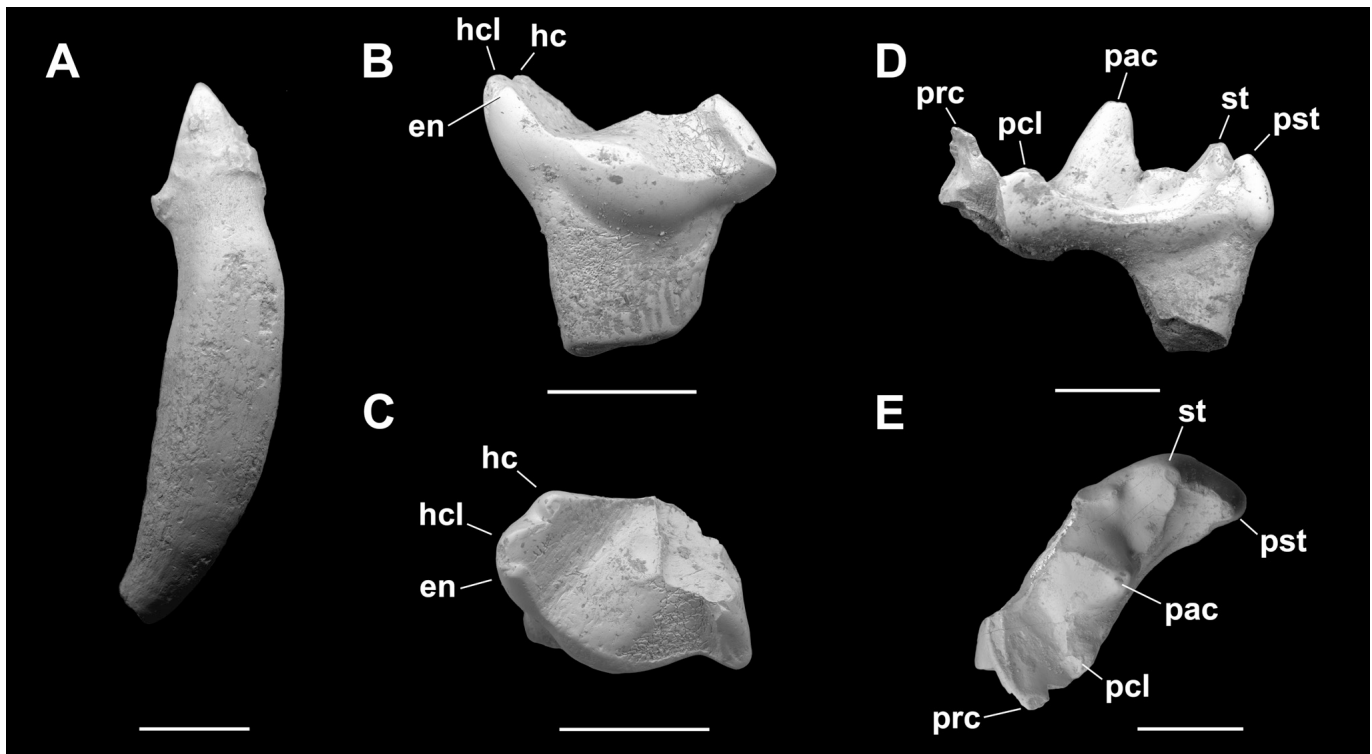**Material**—One ?premolar.

FIGURE 16. Trechnotherian mammals from the Cloverly Formation. **A**, USNM 546705, Spalacotheriidae indet., ?premolar, buccolingual view; **B**, USNM 546728, cf. *Atokatheridium* sp., left lower molar talonid, lingual view; **C**, USNM 546728, cf. *Atokatheridium* sp., left lower molar talonid, occlusal view; **D**, USNM 546657, *Oklatheridium* sp., right M2, anterior view; **E**, USNM 546657, *Oklatheridium* sp., right M2, occlusal view. **Abbreviations**: **en**, entoconulid; **hc**, hypoconule; **hcl**, hypoconulid; **pac**, paracone; **pcl**, paraconule; **prc**, protocone; **pst**, parastyle; **st**, stylocone. Scale bars equal 1 mm.

Description—The specimen (USNM 546705; Fig. 16A) preserves a long, posteriorly curved root and a small crown that bears some resemblance to specimens from the Cedar Mountain Formation (Cifelli, 1999b). Identification of the tooth as a premolar is tentative.

THERIA Parker and Haswell, 1897
METATHERIA Huxley, 1880a
ATOKATHERIDIUM Kielan-Jaworowska and Cifelli, 2001
cf. *ATOKATHERIDIUM* sp.
(Fig. 16B, C)

Locality—USNM Loc. 42183.
Material—One left lower molar talonid.
Description—USNM 546728 is highly worn and lacks most of the trigonid (Fig. 16B, C). It is similar to *Atokatheridium boreni* in having a widely open lingual edge, but differs in that the entoconid is present as a small cusp clustered against the elongate hypoconulid. A steep-walled structure at the anterolingual corner represents the base of the metaconid, which protrudes lingually past the edge of the talonid.

OKLATHERIDIUM Davis, Cifelli, and Kielan-Jaworowska, 2008
OKLATHERIDIUM sp.
(Fig. 16D, E)

Localities—USNM Loc. 42183, 42222.
Material—One partial right M2, one partial right M4, one partial left upper molar, one right lower molar trigonid.
Description—USNM 546657 preserves the anterior two-thirds of a right M2 (Fig. 16D, E). The protocone has a slightly con-vex labial face and connects to a large paraconule that is more lingually positioned than the metaconule. The preprotocrista reaches the parastyle, which is separated from the teardrop-shaped stylocone by a notch. The paracone has a round base, is 1 mm tall, and connected to the stylocone by a distinct preparacrista. USNM 546717 preserves a 1.2-mm-long trigonid. The three cusps are tall, with the metaconid slightly shorter than the paraconid and both significantly shorter than the protoconid. All are externally convex, but the paraconid and protoconid are internally concave. Gaps separate the cusps from one another, so that the cristae do not connect. USNM 546730 represents the anterolabial portion of an upper molar, including the paracone and most of the stylar shelf, which bears a crest along the labial margin. The stylocone is tall with a rounded base, connected to the paracone by a low ridge, and is flanked posteriorly by a small cuspule. USNM 546729 preserves the lingual two-thirds of a right M4. The protocone is quite low and triangular in occlusal view. The two conules are nearly half the height of the protocone and sit along pronounced cristae. Most of the large paracone is visible along the broken margin, adjacent to part of a strongly reduced metacone. The size and morphology of these specimens are comparable to *Oklatheridium* sp. from the Antlers Formation (Davis and Cifelli, 2011).

METATHERIA indet.

Locality—USNM Locs. 42222.
Material—One partial upper molar.
Description—USNM 546718 is a tiny specimen preserving a small protocone and the lingual portions of the metacone and paracone. The weak development of the protocone is consistent with assignment to a metatherian.

TRECHNOTHERIA indet.

Locality—USNM Loc. 42183.

Material—Three lower premolars.

Description—USNM 546735 is a nearly complete, double-rooted tooth with a large primary cusp and small secondary anterior cusp. The primary cusp is anteroposteriorly elongate and flanked by nearly straight anterior and posterior carinae. The anterior carina terminates near the anterior edge of the tooth but does not connect to the secondary cusp. The posterior carina ends at a small bump at the base of the posterior side of the crown. A small basin flanks the secondary cusp on one side only. A similar tooth (USNM 546667) lacks roots and differs in morphology by exhibiting distinct concave areas alongside the carina between the two cusps. In addition, the proportions are slightly less elongate. USNM 546734 may represent p2–3. It has two cusps, the primary about 4 times the height of the secondary, which are connected along a weak carina. The tooth is double-rooted and bears a flat surface along one side between the cusps.

MAMMALIA indet.

Localities—USNM Locs. 42175, 42183, 42222.

Material—Eight partial teeth, seven partial limb elements.

Description—We refer several fragmentary tooth and limb specimens with diagnostic features to Mammalia. The tooth fragments bear multiple cusps and a complex occlusal surface. Some preserve multiple roots. The limb elements preserve their epiphyses.

RESULTS

Additions to Cloverly Formation Vertebrate Diversity

The new material recovered during this study more than doubles the known vertebrate diversity of the Cloverly Formation, from 25 to 51 taxa (Table 2). Many of the added taxa are small-bodied forms. The two VMBs alone produced 43 taxa, including many not documented elsewhere. Among these additions are lonchidiid sharks, several osteichthyans, batrachosauroidid salamanders, a second paramacellodid, two teiids (including the Antlers lizard *P. wilsoni*; Nydam and Cifelli, 2002), multituberculates, and metatherians. Several species occur in both VMBs and at USNM Loc. 42175 but at no other sites visited during this study; examples include *Albanerpeton*, *Zephyrosaurus*, and the hybodontoids. In comparison, turtle and crocodylian remains are nearly ubiquitous, occurring at 17 and 14 sites, respectively.

This study adds significantly to Cloverly mammalian diversity by recovering 77 mammal specimens from at least eight different taxa. Cloverly multituberculates were previously undescribed, but we recognize three distinct genera, each of which is also present in the Cedar Mountain Formation. Of the three previously known mammals, only *Gobiconodon ostromi* is definitively present in our sample, but some of the new alticonodontine and trechnotherian specimens might derive from known taxa (e.g., *Corviconodon* and *Montanalestes*, respectively).

Several Cloverly taxa—*Pseudohypolophus*, an indeterminate cryptodire (Ostrom, 1970), *Ornithomimus*, *Tatankacephalus*, *Acrocanthosaurus*, *Sauroposeidon*, and a ceratopsian—seem to be absent from our samples but could be represented by non-overlapping or poorly preserved specimens in our collection. For example, the indeterminate turtles that Ostrom (1970) identified from humeri (YPM 4900, 4903) could pertain to our Testudinata 'species A,' which is based on carapace fragments. *Tatankacephalus*, *Acrocanthosaurus*, and *Sauroposeidon* could be represented by unidentified elements here referred to Ankylosauria, Tetanurae, and Titanosauriformes, respectively. In order to be conservative with diversity counts, we have defaulted to the minimum number of taxa in each case. We also refrained from counting our indeterminate alticonodontine and trechnotherian mammal specimens as separate taxa.

Nevertheless, a marked enhancement has been achieved in our understanding of the small-bodied vertebrates in the Cloverly fauna, which now display a diversity more typical of Cretaceous terrestrial formations elsewhere. In addition, our samples extend the stratigraphic ranges of many vertebrate taxa within the formation, because many have been recovered from strata not studied intensively by Ostrom (1970:fig. 5). Finally, it is now evident that, at the generic level at least, faunal composition remained relatively consistent during Cloverly deposition (Fig. 17).

Sampling Assessments

Rarefaction analysis of our formation aggregate sample suggests an asymptote of ca. 55 taxa (Fig. 18), indicating that a relatively small number of new species may be recovered from further sampling. The individual rarefaction curves for the two VMB sites are generally similar to the aggregate curve. The USNM Loc. 42183 curve corresponds closely with that for the aggregate sample in both shape and estimated number of taxa. The USNM Loc. 42222 curve parallels these but is notably lower.

A tally of previously published Cloverly macrofossil collections yielded 536 specimens (with associated or articulated remains counted as one specimen), representing 18 taxa. The rarefaction curve for this data set is lower than any of the other sampling curves at equivalent sample sizes (Fig. 18). (By comparison, a sample of 500 specimens from USNM Loc. 42183 would be expected to yield 32 taxa.) USNM Loc. 42175 yielded a much smaller overall sample, so only the rising portion of its curve can be examined, but this resides between the curves for the previously prospected sample and USNM Loc. 42222.

Taxonomic Abundances and Diversities

Based on the total number of recovered elements, osteichthyans are the most abundant major group in the present sample (40% of the total; Fig. 19), although more than half of the specimens are indeterminate scales. Crocodylians are the next most common group, represented primarily by teeth. All four taxa are common, but atoposaurids account for almost half of all crocodylian specimens. Squamates and mammals are the least abundant higher-order groups, together accounting for less than 1.5% of identified specimens. Dinosaurs, turtles, and amphibians each constitute 8–15% of the total, whereas chondrichthyans represent about 3%.

The relative abundances of major vertebrate groups change drastically when the VMB specimens are excluded (Fig. 19). Considering only the surface and non-VMB samples, dinosaurs appear most abundant (36%), followed by turtles (30%). Pholidosaurid teeth and crocodylian scutes are common in surface-collected samples, but crocodylians are less abundant overall, as are osteichthyans. The remaining groups are almost entirely absent, and derive almost exclusively from USNM Loc. 42175. In contrast, the VMB-only sample shows very similar abundances to the aggregate.

Including VMB specimens in the overall faunal count results in increased diversities for all major vertebrate groups except turtles (Fig. 20). Dinosaurs remain the most diverse group, accounting for almost one-quarter of total vertebrate diversity, but the new samples reveal high diversities for Osteichthyes and Mammalia as well. The remaining groups each contribute about 1/12 of overall diversity. Without VMB contributions, dinosaurs account for about two-thirds of total diversity, whereas lizards are entirely absent. Despite being represented by fewer taxa, turtles appear to be more significant faunal components than is the case when VMB data are included.
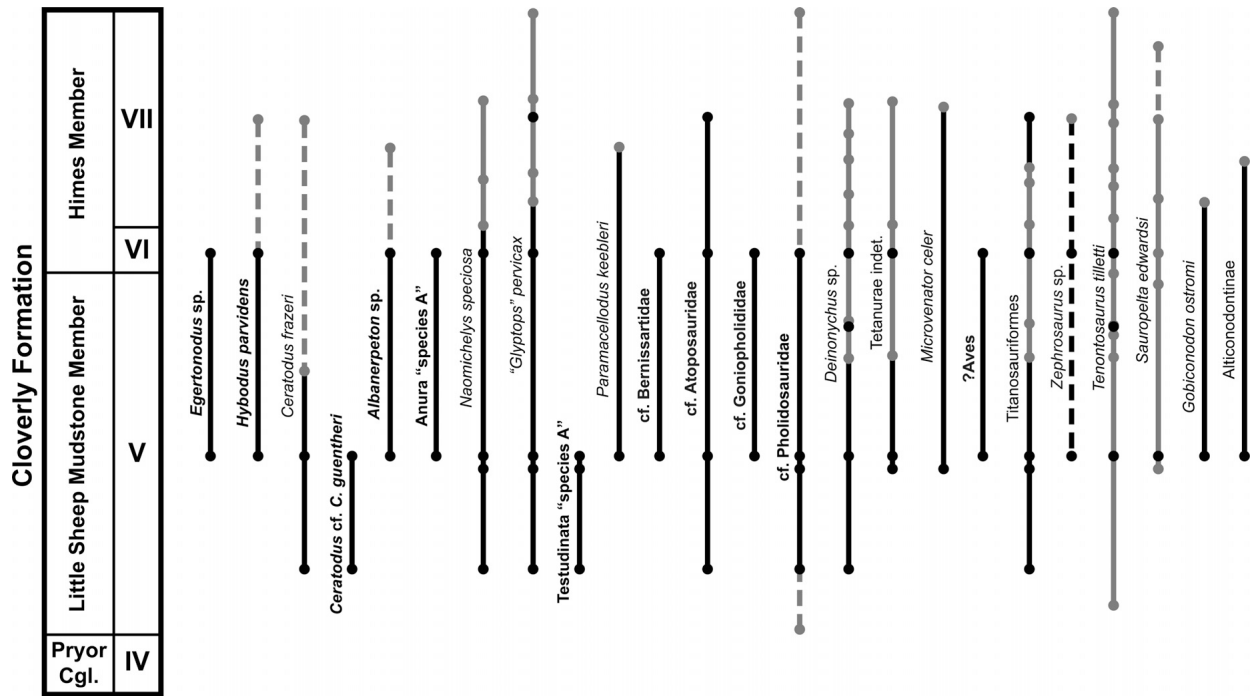
FIGURE 17. Stratigraphic distributions of Cloverly Formation vertebrates. Generalized stratigraphic section showing the approximate stratigraphic positions of vertebrate taxa within the formation (only those occurring at multiple levels are shown). Gray circles and bars show previously reported occurrences and ranges, respectively; black circles and bars show additions from the present study; dashed lines indicate range extensions based on uncertain taxonomic assignments; newly added taxa are shown in boldface.

Paleobiogeographic Relationships

Our new samples suggest that at least 48 genera are present in the Cloverly, 30 of which bear formal names. This includes taxa that are only identified less specifically (e.g., Batrachosauroididae indet.), but which must pertain to at least one genus. This revised Cloverly fauna shares 15 genera with the Antlers Formation, two with the Patuxent Formation, and 13 with the Mussentuchit Member of the Cedar Mountain Formation. However, generic richness for these formations varies: there are 10 formally described genera in the Patuxent but at least 46 in the Mussentuchit and 28 in the Antlers. Comparisons of Sørensen Index values are consistent regardless of how 'permissive' the definition of taxonomic similarity used (higher similarities result from more permissive definitions; Table 3A, B). Comparing Cloverly and Antlers faunas yields the highest Sørensen Index values (0.58/0.53) of any pair, followed by the Cloverly and Mussentuchit (0.51/0.35). In general, the Cloverly, Antlers, and Mussentuchit faunas are more similar to one another than any are to the Patuxent.

DISCUSSION

Paleoenvironmental Interpretation of the Cloverly Vertebrate Fauna

Given the widespread nature of many taxa within the formation (see below), little can be said about Cloverly paleoenvironmental conditions based on faunal composition alone. The Cloverly paleoenvironment and its vertebrate fauna shared much in common with neighboring dinosaur-bearing formations of the Western Interior. The presence of possibly marine or estuarine taxa (e.g., pycnodontiforms, myliobatoids; Maxwell et al., 1997) suggests a setting near a coastal margin, although the occurrence

of many obligate freshwater taxa, particularly amphibians, clearly indicates a predominantly freshwater paleoenvironment.

Both aquatic and semiaquatic forms provide abundant fossil remains without showing evidence for high taxonomic diversities. We may have undercounted these diversities due to the difficulties associated with identifying isolated crocodyliform teeth and osteichthyan scales. But there is also likely a taphonomic bias against preservation of terrestrial individuals, which would have had to survive greater transport before entering these burial systems. Thus, the relative balance between aquatic + semiaquatic taxa (25 if all turtles are included) and terrestrial taxa (26) may be approximately accurate. Although we note the previous speculation that some triconodontans might have been semiaquatic (Slaughter, 1969), crocodylians and turtles represent the primary faunal 'overlap' between the aquatic and terrestrial components of the Cloverly paleoenvironment.

Certain taxa may have been genuinely rare, considering their infrequency across localities and sampling modes, or they may have lived further from the freshwater systems responsible for Cloverly deposition. These include the myliobatoid *Pseudohypolophus*, known from a single Cloverly locality (Maxwell et al., 1997) but present at multiple Trinity Group sites (Winkler et al., 1990) and elsewhere across Aptian–Campanian Western Interior near-shore deposits (Johnson and Lucas, 2002), as well as taxa such as *Microvenator* and *Zephyrosaurus*, represented definitively by very few specimens in our samples. A basal neoceratopsian has also been reported (Maxwell and Cifelli, pers. comm. in Chinnery-Allgeier and Kirkland, 2010), but we recovered no additional remains of this clade. The absence of other taxa, such as pterosaurs, is more likely attributable to preservational or sampling biases, given the ubiquity of the group in Cretaceous terrestrial deposits worldwide (although their remains are often rare and fragmentary).
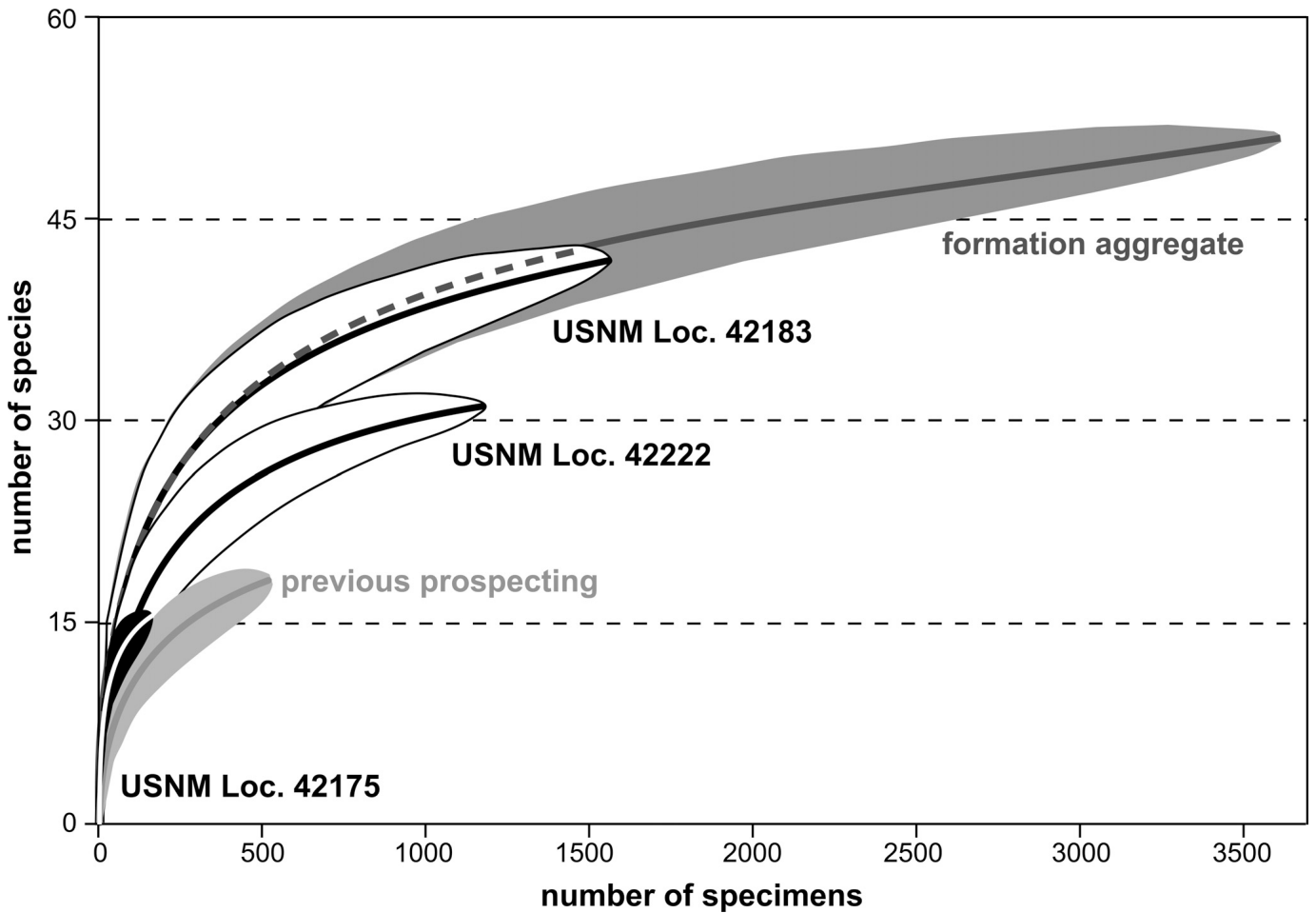
FIGURE 18. Sampling rates of Cloverly vertebrates. Graph showing rarefaction curves (solid lines) for three VMB localities (black and white lines) as compared with those for all previous fossils collected through traditional prospecting (light gray line), and the aggregate total sample for the entire formation (dark gray line, with dashed segment showing continuation behind other curves). Envelopes enclose the 95% confidence intervals for each curve.

Although the above represents a very general assessment of the Cloverly paleoenvironment, it is broadly congruent with those of other terrestrial formations from the Late Jurassic through Late Cretaceous. The importance and diversity of aquatic and semiaquatic taxa in these paleoenvironments are often underestimated due to the difficulties associated with identifying fragmentary remains and the tendency for studies to focus on terrestrial taxa such as mammals and dinosaurs. However, the predominance of aquatic/semiaquatic taxa in most of these paleoenvironments argues for greater effort and attention toward these groups.

Biogeographic and Biostratigraphic Implications

Small-bodied taxa identified in VMBs help clarify the temporal and paleobiogeographic relationships between the Cloverly and other Lower Cretaceous formations in western North America, particularly the Antlers and the Cedar Mountain. Although the common occurrence of dinosaurs such as *Deinonychus* and *Tenontosaurus* supported comparisons between the Antlers and Cloverly formations (Brinkman et al., 1998), the lack of shared lizard taxa led Nydam and Cifelli (2002) to question their temporal equivalence. The recovery of the Antlers lizard *Ptilotodon wilsoni* in our Cloverly samples resolves this concern.

Because the Cedar Mountain Formation was deposited over such a long time interval (at least 27 Ma; Kirkland et al., 1997; Greenhalgh, 2006; Garrison et al., 2007), at least part of it was probably coeval with the Cloverly. Paleontologically, the Mussentuchit Member of the Cedar Mountain shares several multituberculates with the Cloverly. The Mussentuchit scapherpetontid is the earliest occurrence for the group in North America (Cifelli et al., 1999), and a related form may be present in the Cloverly Formation. Recent work suggests that the Mussentuchit Member may be as young as Albian–Cenomanian (Eaton and Cifelli, 2001). The derived lepidosaurs (Evans, 1998) and absence of sphenodontians, along with these faunal commonalities, may support at least an Albian overlap between the upper part of the Cloverly and the Mussentuchit.

Two of the other Cloverly amphibians may also represent earliest occurrences. If the *Scotiophryne* lineage is indeed present, it would predate the next-oldest occurrence by at least 30 million years. Batrachosauroidids are not known elsewhere in North America until the Campanian, although they have been found in Berriasian deposits of England (Evans and McGowan, 2002).
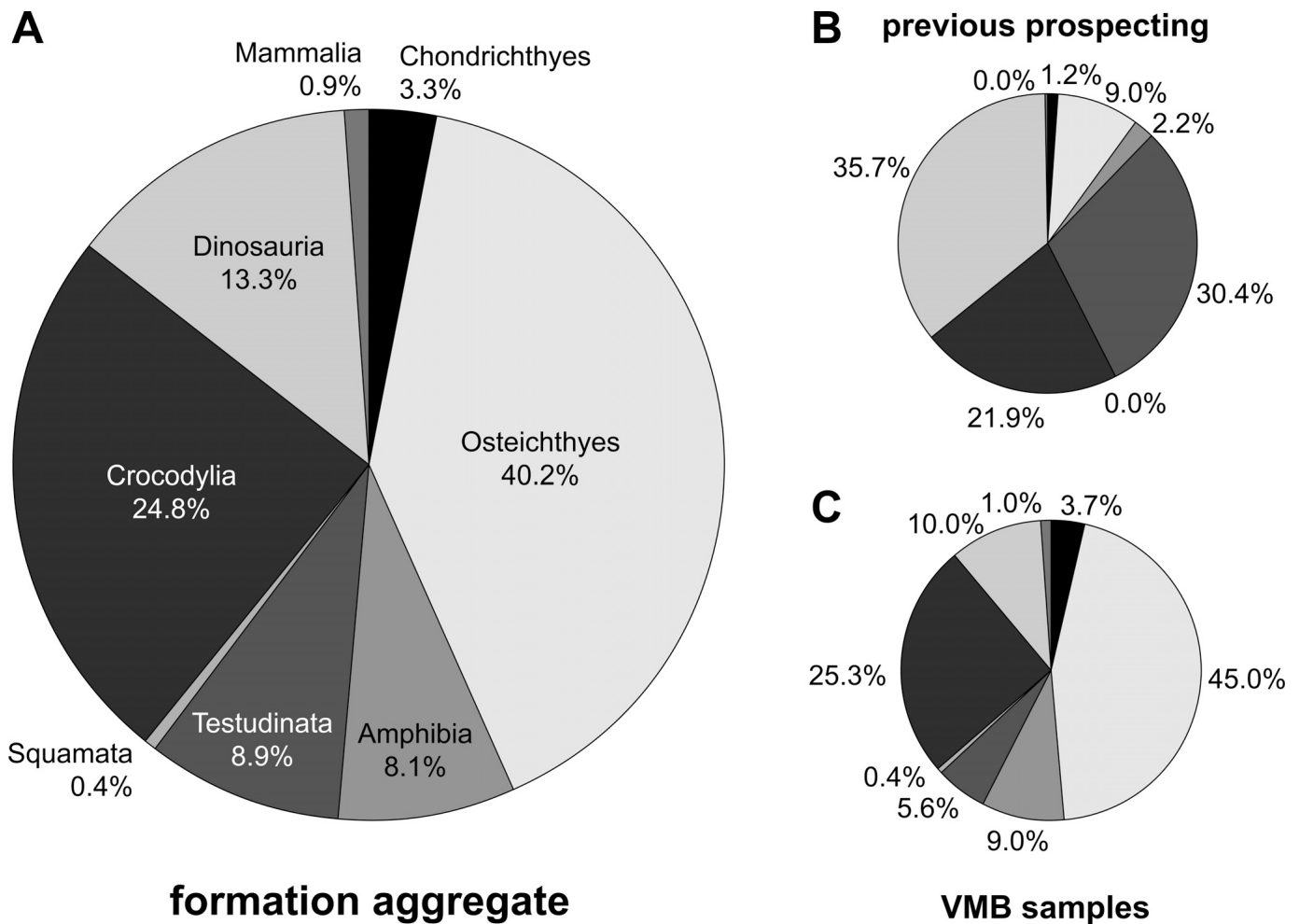
FIGURE 19. Abundances of Cloverly vertebrates. Percentages of total identified specimens for each major vertebrate group are shown for the aggregate total sample (**A**), and as compared with two subsamples: previously prospected specimens (**B**) and VMB specimens (**C**). Note that the order and shading of the graph segments are consistent between all graphs.

Paleobiogeographically, several vertebrate taxa were apparently widespread in both latitude and longitude during the North American Early Cretaceous. Alticonodontine triconodonts and dromaeosaurid theropods ranged over much of the United States, from the Cedar Mountain Formation in the west to the Patuxent Formation in the east. Similarly, *Tenontosaurus* (or a closely related form) is known to occur from Idaho and Montana to Oklahoma and possibly as far east as Maryland, whereas *Acrocanthosaurus* has a slightly smaller documented range. The presence of hybodont sharks in the Cloverly Formation is unsurprising, because the group is known to have ranged along the length of the interior seaway, inhabiting both fresh and saline waters throughout the Western Interior.

The lack of faunal similarity between the Cloverly and Patuxent faunas may be due to geographic (and/or temporal) separation, but Sørensen indices can also reflect sampling bias (Wolda, 1981). In addition to being poorly sampled for vertebrates, the Patuxent Formation yields multiple taxa not identified below the family level, which were therefore omitted from the analysis. Index values between the Cloverly, Antlers, and Mussentuchit strata more likely reflect true faunal similarities. The Cloverly fauna is most similar to that of the Antlers Formation, supporting a previously noted correspondence (Brinkman et al., 1998), whereas the Cloverly and Mussentuchit faunas are somewhat less

similar (Table 3). Indeed, the Mussentuchit fauna is considerably richer than the Cloverly at the genus level but nonetheless shares fewer genera with it than does the Antlers. Common genera between the three faunas support their general temporal synchrony, within which the lower Sørensen indices for the Mussentuchit may reflect paleoenvironmental differences.

Microvertebrate Sampling versus Traditional Prospecting

Cloverly VMBs preserve a host of taxa that have not been recovered through decades of traditional prospecting, and that may not be recoverable even with unlimited time and effort devoted to surface collection. These sites account for much of the newly identified Cloverly species richness, as evidenced by the rarefaction analyses (Fig. 18). Our aggregate curve actually represents only a fraction of our total sample (3704/11,335 identified specimens). Rarefaction could only be applied to specimens identifiable at the lowest taxonomic levels, because the remainder possibly pertained to multiple taxa. Many more fossils recovered via bulk sampling were weathered beyond recognition. The aggregate rarefaction curve, together with the low percentage of specifically identifiable specimens, indicates that thousands of additional specimens would be required to obtain even a small
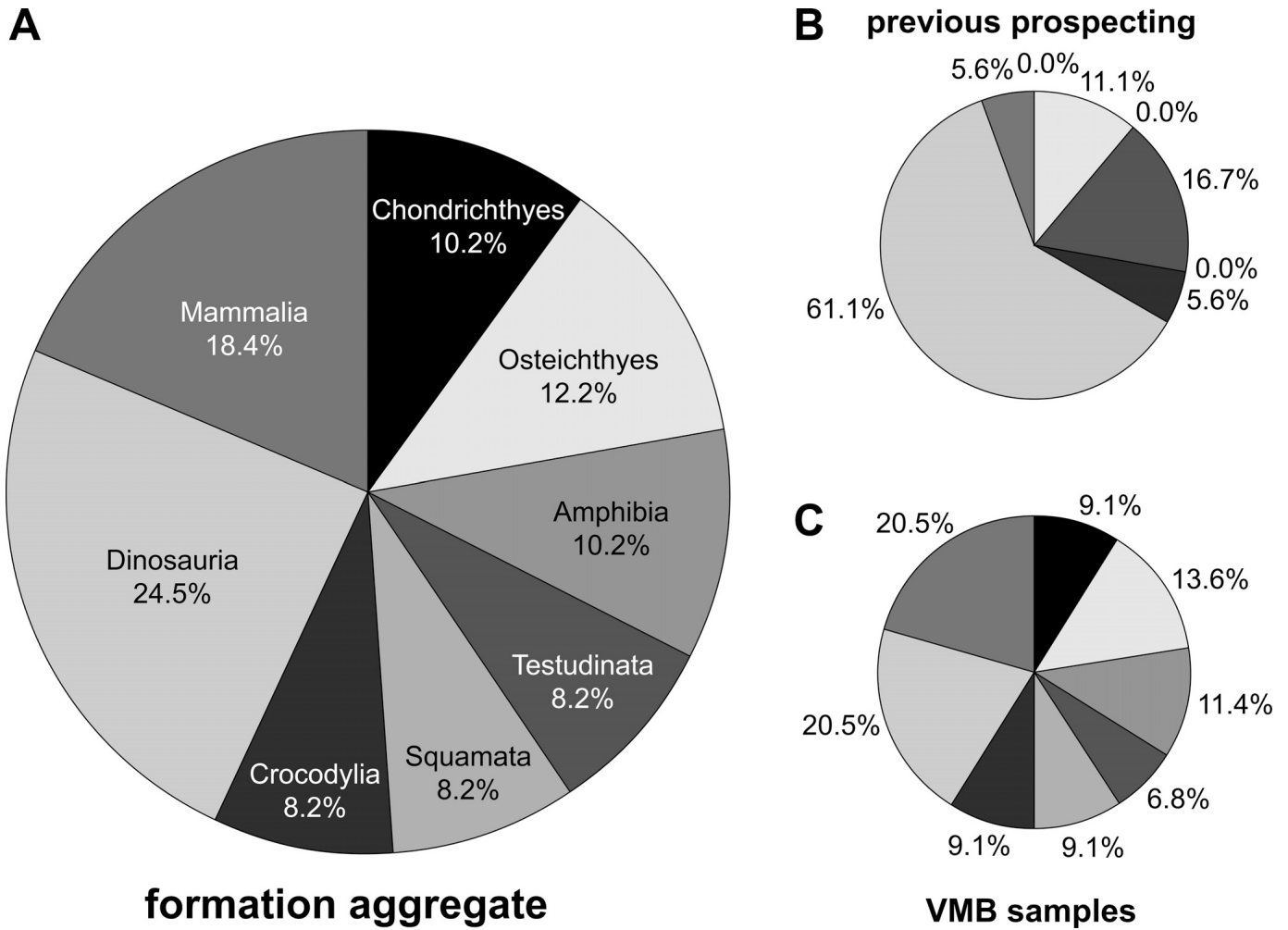
FIGURE 20. Diversities of Cloverly vertebrates. Percentages of total identified taxa for each major vertebrate group are shown for the aggregate total sample (**A**), and as compared with two subsamples: taxa discovered from previous prospecting (**B**) and from VMB localities (**C**). Note that the order and shading of the graph segments are consistent between all graphs.

number of added taxa (cf. Jamniczky et al., 2003). New taxa are unlikely to significantly impact the broader conclusions presented herein.

By offering more complete paleocommunity records, multiple VMBs also enable a level of spatial analysis not possible in a

formation with only macrofossil quarries or surface collections. Our VMBs both preserve nearly the entire known compliment of Cloverly species. However, USNM Loc. 42222 lacks certain terrestrial forms present in 42183. Comparing these sites at equivalent sample sizes confirms this faunal disparity, which might be at-

TABLE 3.   Sørensen Index values for Lower Cretaceous faunas in North America.

	Cloverly (48)	Antlers (39)	Patuxent (20)	Mussentuchit (59)
A				
Cloverly (48)	[1.000]	0.575	0.353	0.505
Antlers (39)	0.575	[1.000]	0.373	0.449
Patuxent (20)	0.353	0.373	[1.000]	0.253
Mussentuchit (59)	0.505	0.449	0.253	[1.000]
	Cloverly (29)	Antlers (28)	Patuxent (10)	Mussentuchit (46)
B				
Cloverly (29)	[1.000]	0.526	0.103	0.347
Antlers (28)	0.526	[1.000]	0.105	0.297
Patuxent (10)	0.103	0.105	[1.000]	0.071
Mussentuchit (46)	0.347	0.297	0.071	[1.000]

Numbers in brackets denote total number of taxa used for comparison. **A**, results using broader definitions of taxonomic similarity. **B**, results using more restrictive definitions of taxonomic similarity.

tributable to paleoenvironmental factors (with USNM Loc. 42222 recording a more fully aquatic environment). Such an analysis would not be possible with most traditionally prospected sites because they preserve few individual occurrences, and therefore must be aggregated to provide sufficient specimen sample sizes for statistical comparisons.

Rather than argue for the elevation of VMB sampling over traditional prospecting, we propose instead that the two are most beneficial when employed in concert. Traditional prospecting offers the best opportunities for recovering large taxa and more complete specimens, and is therefore the primary means to acquire the greatest amount of morphological information. For example, the ability to identify theropod taxa from isolated teeth depends on the availability of specimens that preserve both teeth and other skeletal elements in association or articulation. Yet traditional prospecting can take decades to generate enough specimens to allow statistical analyses of abundances and diversities, and in some settings may never recover enough specimens to afford meaningful intraformational analysis. These issues are best approached through the use of VMBs.

Prospectus for the Cloverly Formation

After more than 75 years of work, the Cloverly Formation continues to yield new paleontological data. However, since 2003 we have prospected nearly all the publicly accessible Cloverly outcrops of the Bighorn Basin, many of them repeatedly, and observed that most fossiliferous deposits weather very slowly. We were able to locate several of Ostrom's quarries from 1962 to 1965, many of which retain the appearance of freshly broken rock despite four decades of aerial exposure. In addition, many macrofossils encountered in the outcrop were either isolated or show significant periburial damage. Given these observations and the comparatively low productivity of the formation in general, it is unlikely that significant new discoveries will be made through traditional methods alone. In order to maximize the productivity of future work and its potential to contribute data toward resolving specific paleontological questions, we offer the following recommendations:

(1) Focus on outcrops that are potentially more fossiliferous, particularly those west and north of Bridger, Montana. None of the Wyoming exposures in the Bighorn Basin can be considered especially promising in this regard, although local concentrations exist.

(2) Prioritize lithologies with the potential to host VMBs, especially in the lowest and highest levels of the formation, where faunal diversity remains poorly understood. Thus far, these are primarily fine-grained sediments such as claystone and mudstones (and therefore interpreted as lower-energy depositional settings).

(3) Collect bulk sediment samples from macrofossil-bearing sites for screenwashing. Although 'blind washing' (Eaton, 2004) may be attempted, the extremely low rate of fossil recovery for most sites suggests that this method is unlikely to be productive in the Cloverly.

CONCLUSIONS

The recovery and analysis of thousands of new specimens from VMBs has substantially improved our understanding of the Early Cretaceous vertebrate fauna from the Cloverly Formation. This is particularly true for the aquatic biota: fossils of aquatic and semiaquatic taxa are abundant and represent derived amphibians and osteichthyans, including families that remained prominent into the Late Cretaceous in North America. Our understanding of the terrestrial community is less significantly changed, but dinosaurs now account for a much smaller percentage of the overall diversity than was previously evident. Thanks to VMB sampling,

the Cloverly vertebrate fauna now appears much more similar in composition to those from other Lower Cretaceous formations in North America, suggesting that the continent was home to broadly similar vertebrate faunas at that time.

Additional insights into the Cloverly vertebrate fauna may yet be gained from a detailed, site-level analysis. The two most productive Cloverly VMBs record 44 vertebrate species, approaching the total number of vertebrates known from the formation, but faunal compositions vary slightly between these sites. Compositional differences between the VMB samples, and differences in the distribution of taxa across the other sites, may reveal aspects of Cloverly paleocommunity structure. The co-occurrence of diverse, presumably sympatric, small carnivores suggests complicated niche partitioning/community assembly processes that may be discernable with further study. A spatial analysis would likely reveal subtle paleoenvironmental variations, including possible estuarine influences, which might explain some of the apparent niche overlap. Finally, a guild analysis could address the overlap between the terrestrial and aquatic systems and the specific ecological roles played by different taxa.

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